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Estimating the relative importance of predator-prey interactions in the provision of marine ecosystem services

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Estimating the relative importance of predator-prey interactions in the provision of marine ecosystem services

by

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Contents

Chapter 1

General Introduction

1.1. Background

Global defaunation and the persecution of predators has led to the 'trophic downgrading' of the biosphere, whereby the reduction in higher-order predators has led to an ecological shift favouring species occupying lower trophic levels (Estes *et al.*, 2011; Dirzo *et al.*, 2014). Historically, removal of higher order predators and megafauna has been more widespread and severe in terrestrial and freshwater systems (McCauley *et al.*, 2015). This has resulted in more homogenisation in terrestrial systems, simplifying food webs, and while marine systems are now experiencing similar pressures (Carr *et al.,* 2003; Madin *et al.*, 2016), they have remained relatively more heterogenous in their predation regimes (Worm *et al.*, 2003; Costa, 2009; Heupel *et al.* 2014). For example, the UK and Ireland historically supported populations of multiple terrestrial quaternary consumers (apex predators), all of which are now extinct, including multiple species of bear (Ball and Owen, 1847; Leonard et al., 2013), grey wolves (Hickey, 2000, 2003), cave lions and cave hyenas (Yalden, 1999). As such, contemporary UK and Irish terrestrial apex predation is limited to tertiary consumers, which are also relatively few in number, comprised predominately of 11 mammal species (Harris *et al.*, 1995) and ~30 bird-of-prey species (Brown, 1976; Ketley, 2021). These predators feed on secondary consumers such as smaller mammals, smaller birds, amphibians and reptiles, of which there are less than 1000 species in the UK and Ireland (Harris *et al.*, 1995; Inns, 2011; McInerny *et al.*, 2018).

In contrast, UK and Irish waters still host marine quaternary consumers, such as orca (*Orca orcinus*), (Evans, 1988) and thresher sharks (*Alopias vulpinus*), (Smith et al., 2008), as well as many tertiary consumer species. For example, there are over 50 chondrichthyan species in the UK (Ellis *et al.*, 2005), the majority of which are tertiary consumers, reaching trophic levels

greater than four (Cortés, 1999; Ebert and Bizzarro, 2007), as well as multiple tertiary predators within the Osteichthyes (CEFAS, 2007), Cephalopoda, Pinnipedia and Cetacea (Howson and Picton, 1997).

Degraded terrestrial systems in the developed world generally now host few quaternary and tertiary consumers (Estes *et al.*, 2011; Rao, 2018; Smith *et al.*, 2018), whilst marine systems can host relatively diverse guilds of tertiary consumers, as evidenced by resource partitioning and sympatry across marine predator taxa, including, but not limited to, cetaceans (Bearzi, 2005; Friedlaender *et al.*, 2009), pinnipeds (Saporiti *et al.*, 2016), osteichthyans (Ross, 1986; Crow *et al.*, 2010; Bowen *et al.*, 2013), cephalopods (Valls *et al.*, 2017), brachyurans (Hines, 1982; Griffin *et al.*, 2008; Takeda, 2010) and elasmobranchs (Platell *et al.*, 1998; Navarro-González *et al.*, 2012; Tilley *et al.*, 2013). This resource partitioning facilitates maintenance of trophic overlap, (i.e. the shared use of food resources, among marine predator guilds) (e.g. Vaudo and Heithaus, 2011; Yick *et al.*, 2011; Shaw, 2013; Varghese *et al.,* 2014). By their nature, these guilds contain redundant species, as they contain species that overlap geographically and trophically. While species within these guilds may show some redundancy in their resource and space usage, they are still different species with variations in their behaviour and biology. Thus, the removal of one or more redundant species can still degrade a system and reduce its overall resilience and multiple redundant species can buffer ecosystems (Biggs *et al.*, 2020). However, the effects of trophic overlap, resource partitioning and redundancy on predator-prey interactions are under-studied, with few empirical studies directly investigating functionally redundant predators (Chalcraft and Resetarits, 2003; Biggs *et al.*, 2020;), especially in marine systems (Guillemot *et al.*, 2011).

Animals exist in environments consisting of a patchwork of constantly fluctuating perceived predation risk, best summarised as 'Landscapes of Fear' (Laundré *et al.*, 2010). Within these landscapes of fear, animals encounter varying levels of habitat availability and complexity, resource availability and predation risk (Brown and Kotler, 2004; Hughes and Grabowski, 2006; McArthur *et al.*, 2014; Miller *et al.*, 2014; Schmidt and Kuijper, 2015; Gaynor *et al.*, 2019). These components are driving factors of the 'ecological context' in which animals behave, influencing important behaviours such as foraging and anti-predator responses (e.g. Fu *et al.*, 2015). Landscapes of fear act as the underlying ecological topography in which predator-prey interactions occur and form 'peaks and valleys' of predation risk as described by Laundré *et al.* (2010). As such, fear can be considered an environmental variable, similar to temperature or rainfall, effecting the composition of ecological communities (Laundré *et al.*, 2010; Matassa and Trussel, 2011; Fraker and Luttbeg, 2012; Nifong and Silliman, 2013; Zanette and Clinchy, 2017). See Figure 1.1 for a visualisation of a landscape of fear.

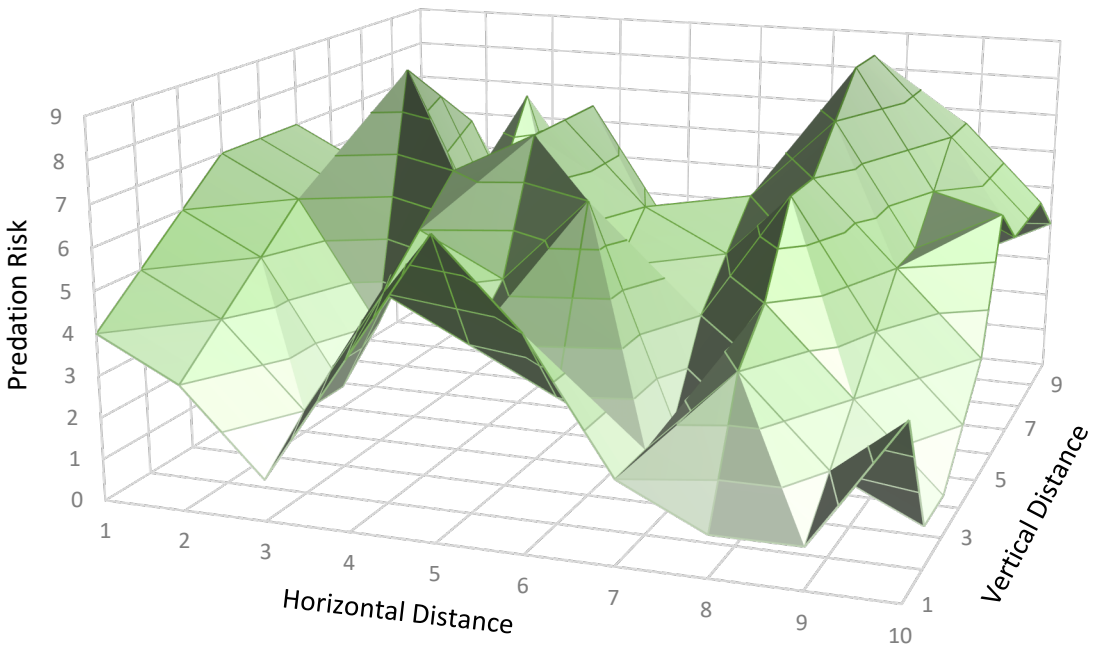

Figure 1.1. Theoretical 3D Surface graph visualising the spatial variation in predation risk encountered by animals in the wild (i.e. a landscape of fear). Image created by thesis author. The spatial fluctuations in predation risk can be caused by changes in factors such as predator presence and density, shelter availability/habitat complexity, conspecific presence and density, and conspecific vigilance.

Trophic downgrading in terrestrial systems has led to the degradation of these landscapes of fear. For example, the extirpation of large predators from Yellowstone National park caused the large herbivore species such as elk and bison to be released from the fear of predation, and the subsequent reintroduction of wolves re-established a functioning landscape of fear (Laundré *et al.*, 2001). The reintroduction of wolves caused a trophic cascade, whereby herbaceous plant species benefitted from a decrease in herbivory due to changes in herbivore behaviour and abundance and coyote mesopredators altered their behaviour to avoid wolves in open areas (Miller *et al.*, 2012). Similar cascades have been observed in marine systems. For example, sharks have been shown to have cascading effects which alter fish size and

community structure on reefs (Barley *et al.,* 2017) and they have been linked to fear-release (Frid *et al.,* 2008).

Cascades can be classified as 'transient' or 'intransient', as described in Barrios-O'Neill *et al.* (2017), which introduced the 'Transient Keystone Concept'. As Barrios-O'Neill *et al.* (2017) discussed, intransient keystone cascades are those which require the ongoing pressure of a keystone predator to sustain the cascade, while transient keystone cascades occur when the recovery of a basal species reaches a point at which it can facilitate its own ongoing recovery, reducing reliance on the keystone predator. For example, even in instances where mature forests are re-established, a lack of predators can cause herbivores such as elk and deer to continue to hinder tree recruitment (Waller *et al.*, 1997), showing the intransient nature of wolf-elk cascades, and identifying wolves as intransient keystone predators. In contrast, Barrios-O'Neill *et al.* (2017) showed that a cascade caused by an elasmobranch predator, the skate species *Raja microocellata*, was transient, as the benefits of predator presence on mussel recruit survival diminished in the presence of a reef structure. This identified *R. microocellata* as a transient keystone predator in this context. Identifying whether marine predator species act as transient or intransient keystone predators can aid future ecosystem management efforts as intransient cascades are more vulnerable to predator extirpation, while transient cascades are, by their nature, more resilient once the basal species has recovered. Misunderstanding whether a cascade is either transient, or intransient, can thus be problematic for the development of effective management plans. For example, an intransient keystone predator would require stronger measures and a likely indefinite management period to ensure ecosystem health, compared to a transient keystone predator, which once it had been managed to a certain threshold of recovery, would cause a cascade that would maintain ecosystem health with considerably less management required. As such,

incorrectly determining or completely failing to determine the transience of a keystone predator could lead to a total failure in management efforts, wasting time and resources.

Keystone predators suppress mesopredators to the benefit of multiple other species (Letnic and Dworjanyn, 2011; Brassine and Parker, 2012; Gordon *et al.*, 2015;) . For example, alligators supress crab mesopredators, preventing the degradation of basal species such as mussels (Nifong and Silliman, 2013) and dingoes suppress mesopredators in arid environments, to the benefit of small rodents (Letnic *et al.*, 2009). This is an important regulatory function that keystone predators provide, influencing mesopredator abundance, distribution and population dynamics (Berger and Conner, 2008; Letnic *et al.*, 2011; Newsome *et al.*, 2017). In contrast, when keystone predators are extirpated from a system, the subsequent release of their prey from the fear of predation is known as 'mesopredator release', a phenomenon that has been observed globally (Prugh *et al.*, 2009; Ritchie and Johnson, 2009; Estes *et al.*, 2011). As such, identifying predators that can suppress mesopredators has the potential to enhance management efforts, as mesopredator suppression by higher predators can prove more cost effective and efficient than human control, as Prugh *et al.* (2009) discussed in their review of mesopredator research. Recently, there have been significant breakthroughs in research investigating predator control of herbivorous species however, key scientific question still remain with regards to predator control of mesopredators as identified in an extensive review and synthesis by Ritchie and Johnson (2009).

While instances of mesopredator release have been identified in multiple terrestrial systems (e.g. Ritchie and Johnson, 2009; Brook *et al.*, 2012; Hollings *et al.*, 2014; Gordon *et al.*, 2017; Krofel *et al.*, 2017; Jachowski *et al.*, 2020;), marine studies are uncommon and rarely use

direct lab-based experiments to investigate mesopredator suppression by higher predators. For example, mesopredators have been suggested as a major contributors to mussel declines in Scandanavia, but the evidence is broad-scale and equivocal (Christie *et al.*, 2020) and other previous marine research has relied on simulated predator-prey models limited to a small number of species interactions (e.g. Frid *et al.*, 2008).

When accounting for the effects of mesopredators on basal species, insights from invasion ecology can be of great use, as in some instances invasive species and those released from the fear of predation bear similarities. For example, while the phenomenon is not ubiquitous, there are instances where invasive species can benefit from predator naïveté and/or a lack of natural predators, leading to a reduction in predation pressure (Colautti *et al.*, 2004; Sih *et al.*, 2010). Thus, methods from invasive research are used to investigate the impacts of invasive species, such as functional response analyses.

Animals produce both behavioural (Cooper, 2000; Altendorf *et al.*, 2001; Kelley and Magurran, 2003; Lehtiniemi, 2005) and physiological responses (Gabrielsen and Smith, 1995; Slos and Stoks, 2008; Clinchy *et al.*, 2013) to fear. Some animals can display ambiguous behaviour during predator-prey interaction, highlighting the efficacy of physiological research. For example, multiple species display behavioural freezing known as 'tonic immobility' as an anti-predator response (O'Brien and Dunlap, 1975; Gallup, 1977; Erhard *et al.*, 1999; Edelaar *et al.*, 2012). To an observer, it would appear as though an animal engaged in tonic immobility is either doing nothing or has frozen in response to fear, preventing overstimulation and loss of energy. However, it can be difficult to empirically assess energy loss and stimulation unless behavioural data is combined with physiological data. For example, an investigation into the cardiac activity of rabbits during periods of tonic immobility

showed that rabbits display bradycardia (slowing of the heart rate) and arrythmia (inconsistent heart beats) during tonic immobility (Giannico *et al.*, 2014).

Cardiac responses such as these have associated costs, as cardiac activity is intrinsically linked to metabolism, stress and health in animals (Galosy *et al.*, 1979; Sgoifo *et al.*, 1999; von Borell *et al.*, 2007). Thus, cardiac response to predator-induced stress is of great value to ecological research. As Clinchy *et al.*, (2013) highlighted, there are few empirical studies documenting physiological stress in the context of predation risk. Additionally, cardiac studies using marine crustacean species are limited and tend to use invasive techniques (e.g. Bierbower and Cooper 2009; Burnovicz *et al.* 2009; Forgan *et al.* 2014; Hourdez 2018), which have the potential to skew results as the stress caused by the invasive procedures could cause pain or discomfort. There is a growing body of evidence that crustaceans can feel pain and experience anxiety states and prolonged discomfort (Elwood, 2019a, 2019b), meaning that this should be taken into consideration in ongoing crustacean physiological research.

Predator-prey interactions can provide multiple ecosystem services, from nutrient cycling (Schmitz *et al.*, 2010; Williams *et al.*, 2018), to the structuring of communities through top-down control (Shears and Babcock, 2002; Boaden and Kingsford, 2015). Mesopredator suppression and trophic redundancy are examples of these ecosystem services. For instance, mesopredator suppression by keystone predators has direct socioeconomic benefits that have been identified in terrestrial and marine systems, enhancing fisheries and reducing agricultural losses (Baker *et al.*, 2008; Gregr *et al.*, 2020). Understanding the effects of functional redundancy and/or functional diversity is important as functional redundancy can bolster ecosystem resilience and stability. Ecosystem stability is the capacity for an ecosystem to resist change in the first place, while ecosystem resilience is the ability of ecosystems to

recover from change. Redundancy can bolster resilience and stability by providing 'backup species' (Lawton and Brown, 1994; Rosenfeld, 2002; Chalcraft and Resetarits, 2003; Jaksic, 2003; Ulanowicz, 2018; Biggs *et al.*, 2020). This redundancy can buffer ecosystems, dampening negative cascading effects (Liu *et al.*, 2016) and reducing ecosystem vulnerability to extinction cascades (Sanders *et al.*, 2018).

1.2. Study site and local relevance

The experiments presented in this thesis were carried out in the locality of Strangford Lough, which became Northern Ireland's first Marine Conservation Zone in 2013 (Audit Office, 2015). Strangford Lough is a semi-closed marine basin that historically hosted extensive biogenic horse mussel (*Modiolus modiolus*) reefs, which were found to be severely degraded in the 1990s due to trawling and dredging activity (Audit Office, 2015). Simultaneously, Strangford Lough experienced the extirpation of a top predator, the flapper skate (*Dipturus intermedia*), a keystone species (Barrios-O'Neill *et al.,* 2017). Biological surveys after these disturbances found an increase in the abundance and prevalence of mobile scavengers and mesopredators and a decrease in slow-moving and sessile basal species (Strain *et al.*, 2012). This evidence suggests that Strangford Lough has undergone a regime shift, caused by the degradation of basal species and the removal of keystone predator species. This is a phenomenon observed across other systems (Heck and Valentine, 2007; Kramer and Heck, 2007; Smith, Hunter and Smith, 2010, Conversi *et al.* 2015). As such, this thesis investigated the ecosystem service provision of native elasmobranch predators to better understand how such species may be used to mitigate the effects of such a regime shift. To accomplish this, the research presented here focused on mesopredator suppression caused by predator-induce stress (fear).

Chapters 2 and 3 aimed to investigate the effects of predator and prey identity, as well as habitat complexity on mesopredator suppression. From a Marine Protected Area management perspective, this was important as understanding how different species respond to the same stimulus can help to identify whether a particular management

measure will be effective across multiple species, and how habitat complexity can mediate these effects.

Subsequently, Chapter 4 was designed to utilise techniques from invasive species research to investigate the effects of spatial availability and conspecific presence on mesopredator feeding. The aim of this research was to enhance the understanding of the role which conspecifics play in the feeding success of decapod crustacean mesopredators. Combining the findings of Chapter 4 with those of Chapters 2 and 3 can enhance the understanding of how brachyuran mesopredators use space, react to conspecifics, and respond to predators while feeding.

Finally, Chapter 5 used cardiac recording techniques to explore the underlying physiological response of brachyuran mesopredators to predator cues. This study tested for differences in how individuals reacted physiologically to predators and non-predators. This research, combined with that of Chapters 2-4, aimed to provide a holistic understanding of the interactions between brachyuran mesopredators and elasmobranch predators. In relation to Strangford Lough, where an increase in such mesopredators has been observed, this research could be used to inform future management strategies, though it is limited in its prescriptive power.

Chapter 2

Trophic Redundancies, Predator Identity and Fear Induced Mesopredator Suppression by Transient Keystone Predators

Impact statement

This chapter was impacted by delays due to several issues outside of my control, including the COVID-19 pandemic, which led to the inability to secure species I initially wanted to investigate, such as the crab specialist predator, the starry smooth-hound *Mustelus asterias*. This would have allowed for further determination of trophic redundancy vs trophic diversity effects by comparing a highly specialist elasmobranch predator to more generalist species. However, this was not possible.

Additionally, another thesis chapter, complimentary to this one, was planned, which would have consisted of a catch-tag-release and recapture population survey of crustacean mesopredators in Strangford Lough, comparing areas inside and outside of a fisheries no-take zone within a Marine Conservation Zone. COVID-19 restrictions prevented the data collection for this planned chapter from taking place, meaning the entire chapter was lost. Some supplementary data had already been analysed for this lost chapter, involving density calculations for mesopredators observed in video trawls collected by the Agri-Food and Biosciences Institute (AFBI), see Chapter 3 impact statement for how this data informed other work.

2.1. Abstract

Predators alter the behaviour of their prey species non-consumptively through fear of predation. Here, lab-based behavioural experiments incorporating two different benthic elasmobranchs (*Scyliorhinus stellaris* and *Raja clavata*) show that they can suppress the feeding of a brachyuran crustacean (*Carcinus maenas*) on post-juvenile mussel spat (*Mytilus edulis*). *C. maneas* is a well-known mesopredator and mussel consumer and understanding methods for suppressing its feeding can provide insight into how to reduce or reverse the negative cascading effects of mesopredator release within degraded systems. My results showed that, while crab feeding was reduced in the presence of both elasmobranch species, there was no significant difference between the two predator treatments. This is evidence of potential trophic redundancy, which can enhance ecosystem resilience. Furthermore, when mature mussel reef was present, crab mussel consumption was reduced and reef presence mitigated the effects of predator presence, which is evidence of transient keystone predator effects. When predators were present, they also decreased the instance of reef dismantling by the crabs. No crabs were consumed at any point during the experiments, making all effects non-consumptive. These results highlight the importance of both top-down and bottom-up effects in combination to maintain reef integrity and enhance spat survival, as well as the importance of non-consumptive predator-prey interactions. This is evidence that the preservation of a healthy and diverse predator population can aid in retaining the top-down pressure and trophic redundancy biodiversity and ecosystem stability and potentially facilitate the growth and renewal of biogenic reefs.

2.2. Introduction

2.2.1. Transient Keystone Species

Predators can play pivotal roles as keystone species, enhancing biodiversity, reducing disease, providing ecosystem stability and a number of other key ecosystem functions (Stier *et al.*, 2016). Recent research has shown that 'transient, ecosystem-mediated keystone effects' have been overlooked and play an important role in predation ecology (Barrios-O'Neill *et al.*, 2017). The keystone species concept asserts that there are species that define an ecosystem and, if extirpated, the ecosystem would be dramatically altered, or even collapse over time. This concept was initially developed by Robert Paine (Paine, 1969), then caveated in later years (Paine, 1995) to highlight the need to consider multi-species approaches to keystone species management. Consequently, the keystone species concept has shaped ecological research, influencing how species interactions and their relative importance are currently framed and understood (Mills and Doak, 1993; Lawton and Brown, 1994; Davic, 2003). It has proved to be a useful tool for describing and defining the role of predators within their ecosystems.

The effects of predators can be context-dependent (Haswell *et al.,* 2017), with keystone effects being mitigated by another factor/species, a phenomenon that has been described as the 'transient keystone concept' (Barrios-O'Neill *et al.*, 2017). As described in Barrios-O-Neill *et al.* (2017), a transient keystone predator displays a keystone effect, (e.g. mesopredator suppression to the benefit of a basal prey species), until another factor, such as habitat availability, takes primacy in the interaction. The increased habitat availability increases shelter for the mesopredator and the basal prey species, mitigating the effects of the

keystone predator, thus making the predator effects transient. Essentially, transient keystone predators and basal species form an important keystone-basal feedback loop that regulates predator-prey interactions and provides the context in which they occur (Chamberlain *et al.*, 2014; Haswell *et al.*, 2017). This feedback loop combines top-down (predator mediated) pressure from predation on the mesopredator and bottom-up (basal mediated) pressure from the basal species increasing shelter for the mesopredator. The combination of top-down and bottom-up pressures then structure ecological communities by altering species abundance, distribution and behaviour (Seitz and Lipcius, 2001; Burkholder *et al.*, 2013; Lynam *et al.*, 2017; Welti *et al.,* 2020). Consequently, many predators that would not traditionally be considered keystone species could be considered transient keystone species under the right ecological conditions.

2.2.2. Fear of predation and non-consumptive effects

Consumptive effects are those that occur when a predator feeds directly on a prey animal, and non-consumptive effects are effects that reduce prey fitness without prey fatality caused by consumption (Hoki *et al.*, 2014). As such, predators can influence prey abundance and behaviour, either through direct predation or through the fear of predation, via either consumptive or non-consumptive effects, or a combination of both (Matassa and Trussel, 2011; Haswell *et al.*, 2017). Non-consumptive effects can be so powerful that the fear of predators alone is enough to alter prey behaviour and cause cascading effects through trophic levels (Trussell *et al.,* 2006a; Suraci *et al.,* 2016;). Fear alters prey behaviour and risk assessment over time (McArthur *et al.*, 2014; Guariento *et al.*, 2018) and can directly reduce prey growth and overall fitness (Preisser *et al.,* 2005; Schmidt and Kuijper, 2015), making non-consumptive effects such as fear important ecological drivers.

Recent studies have highlighted the importance of taking into account non-consumptive effects when studying predator-prey interactions, as they can have the same, if not greater impacts than consumptive effects (Hoki *et al.*, 2014; Ingerslew and Finke, 2018). Accounting for non-consumptive effects when studying predator-prey interactions can provide greater ecological insight than addressing consumptive effects alone, enhancing the explanatory power of studies that record non-consumptive effects. For example, Atuo and O'Connell (2017) found that a combination of direct losses by predation mortality (consumptive) and resource avoidance due to perceived predation risk (non-consumptive) from Red- tailed Hawk (*Buteo jamaicensis*) and Northern Harrier (*Circus cyaneus*) drove reductions in Northern Bobwhite (*Colinus virginianus*) quail bird productivity.

2.2.3. Mesopredator release and bivalve molluscs

Mesopredator release occurs when predators are extirpated from an ecosystem, or their populations are severely reduced, and their prey are released from the fear of predation (Frid *et al.*, 2008; Ritchie and Johnson, 2009; Krofel *et al.*, 2017). This fear release can lead to negative cascading effects, as the increased abundance of mesopredators caused by release can impact prey species. As such, understanding how predators can suppress mesopredators to the benefit of prey species can provide insight into enhancing biodiversity and ecosystem stability. For example, the presence of alligators has been shown to enhance mussel and snail survivability in salt marshes by suppressing blue crab mesopredators (Nifong and Silliman, 2013). Increased survivability of these two animals was shown to enhance the 'potential for both grazing and mutualism to occur in this food chain', improving ecosystem functioning.

Bivalve molluscs are ecosystem engineer species, forming biogenic reefs (Ritchie and Johnson, 2009). Thus, habitat complexity and availability can be reduced by mesopredator release, as

seen in crustacean-bivalve interactions, whereby crabs feed upon juvenile oysters (Hill and Weissburg, 2013; Kulp and Peterson, 2016) and mussels (Smallegange and Van Der Meer, 2003; Capelle *et al.,* 2016), degrading biogenic habitats. Thus, the ecosystem service provided by predators in the form of mesopredator suppression can be of utility in instances of bivalve degradation where mesopredator populations expand rapidly and without mitigation (i.e. in instances of mesopredator release).

2.2.4. Trophic redundancy, guilds and marine elasmobranchs

Trophic redundancy occurs when two or more species with distinct life histories have overlapping dietary niches (e.g. Matich *et al.*, 2017; Machado *et al.*, 2020). Trophic redundancy can lead to shared resource use and niche partitioning by animals (Varghese *et al.*, 2014; Naman *et al.*, 2019), leading to researchers grouping multiple species into 'trophic guilds'. A trophic guild is any number of species that use the same resource, or exploit a range of resources in a similar way (Simberloff and Dayan, 1991). Trophic redundancy, and by extension, trophic guilds, can reduce vulnerability to extinction cascades (Sanders *et al.*, 2018), enhance biodiversity and thus, ecosystem reliability (Naeem and Li, 1997) and stability (Ulanowicz, 2018). Thus, when investigating the effects of multiple predators, determining trophic redundancy vs trophic diversity can be crucial to predicting the effect of a predator on its community (Chalcraft and Resetarits, 2003).

Terrestrial systems have historically experienced greater levels of defaunation and anthropogenic pressure than aquatic systems (McCauley *et al.*, 2015), leading to the homogenisation and simplification of terrestrial predator regimes while aquatic systems have retained higher predator diversity (Cox and Lima, 2006). As such, marine systems display high levels of redundancy and guild formation, particularly among elasmobranch species (Navarro-

González *et al.*, 2012; Varghese *et al.*, 2014; Navia *et al.*, 2017). The redundancy and guild formation displayed by elasmobranchs can lead to them occupying multiple roles within an ecological community throughout their life history (Hussey *et al.*, 2015; Kiszka *et al.*, 2015; Roff *et al.*, 2016). They achieve this through mechanisms such as trophic plasticity, and switching prey and habitat use based on ecological context (Drymon *et al.*, 2012; Kiszka *et al.*, 2015). This makes elasmobranchs appropriate models when investigating the effects of predator-prey interactions and redundancies.

2.2.6. Aims and objectives

This study quantified the variation in crab feeding in response to the presence of two biologically distinct, but functionally similar, elasmobranch predators, and to evaluate the effects of biogenic reef presence on these predator-prey interactions. The objective was to record the number of post-juvenile *M. edulis* spat consumed by *C. maenas* crabs when elasmobranch predators and reef were present/absent. Elasmobranch and reef free controls were included. The number of spat consumed within three hours was the metric for these experiments.

2.2.7. Hypotheses

It was hypothesised that crab consumption would be altered by both predator presence and reef presence. It was predicted that crab consumption would be significantly lower in treatments containing predators and/or reef compared to the controls, based on previous findings from Barrios O'Neill *et al.* (2017). It was also predicted there would be no significant difference between the two elasmobranch species treatments, this prediction was based on the trophic overlap observed between the *Scyliorhinidae* and *Rajidae* (Compagno, 1984;

Snowden, 2008). It was further hypothesised that predator presence would impact reef dismantling by the crab, with the frequency of reef dismantling decreasing when a predator was present, this was based on dismantling behaviour observed in pilot studies and a search of the scientific literature did not produce any studies that recorded this behaviour.

2.3. Methods

2.3.1. Species chosen

Here, the elasmobranch species *Raja clavata* and *Scyliorhinus stellaris* were chosen to investigate potential transient keystone effects and trophic redundancies. While related, *R. clavata* and *S. stellaris* have distinct life histories, with one being a member of the *Rajidae* (skates) and the other being a member of the *Scyliorhinidae* (catsharks). However, they display overlaps in both diet and distribution (Compagno, 1984; Snowden, 2008). Furthermore, according to diet studies, *R. clavata* occupies a trophic level of 3.8 ± 0.2 (Palomare and Sa-a, 2008) and *S. stellaris* occupies a trophic level of 4.0 ± 0.3 (Sa-a *et al.,* 2008). This made it likely that these two elasmobranchs displayed some level of trophic redundancy, but as Chalcraft and Resetarits (2003) highlighted, redundancy should be investigated and not assumed. While there were variations in their dietary preferences, both of the elasmobranch species chosen are known to feed on brachyuran crustaceans (Šantić *et al.*, 2012; Caut *et al.*, 2013), common mesopredators, and thus, were likely to cause fear in a brahcyuran mesopredator.

The readily available native brachyuran crab *Carcinus maenas* was chosen as the mesopredator for my expeiments. Despite its prolific use in scientific studies, as evidenced by an extensive review conducted by Leignel *et al.* (2014), a thorough search of the scientific literature did not yield a study that provided a definitive trophic level range for *C. maenas* . However, *C. maenas* is an opportunistic scavenger and generalist predator (Young and Elliott, 2020), mesopredator and secondary consumer, likely occupying trophic levels between 2 and 3. Thus, it was an apporopriate mesopredator model for my study.

C. maenas is also a voracious predator of mussels, preferring them over more robust bivalves such as oysters (Capelle *et al.*, 2016; Campbell *et al.*, 2019) and specifically targeting smaller, juvenile mussles (Smallegange and Van Der Meer, 2003). Thus, the blue mussel *Mytilus edulis* was chosen as my basal prey species. *M. edulis* mussel beds are associated with many epifuanal species (Saier, 2002) and increased habitat availability/complexity (Norling and Kautsky, 2007). This made *M. edulis* an appropriate basal species for investigating the effects of mesopredator suppression on basal species.

2.3.2. Animal Collection and husbandry

Captive reared *Raja clavata* (*N* = 3) and *Scyliorhinus stellaris* (*N* = 3) were obtained from Exploris Aquarium, Portaferry, Northern Ireland. *R. clavata* individuals were within the size range 60-80cm long and *S. stellaris* individuals were within the size range 100-120cm long. The standardised elasmobranchs sizes reflected crabs' capacity to assess predator body size (Hill and Weissburg, 2014). Each elasmobranch individual was used for eight randomly allocated replicates.

Elasmobranchs were maintained individually in outdoor flow-through tanks (2.2m x 1.2m x 1m) with mesh lids, supplied with sand-filtered seawater. Following the guidelines from the Elasmobranch Husbandry Manual II (Smith *et al.*, 2017), tanks were enriched with sand, rocks and seaweed to reduce stress. *R. clavata* and *S. stellaris* were fed *ad libitum* with Atlantic herring (*Clupea harengus*), using a mixture of feeding techniques, both allowing food to fall to the bottom of the tank for foraging enrichment and feeding via pole feeders to ensure consumption. Excess food was removed from the tanks if not eaten within 24 hours. Elasmobranchs were not fed 24 hours prior to experiments to mitigate the impact of olfactory cues from their food. Elasmobranchs were given respite days to ensure regular feeding and

to reduce stress. Individuals were kept for two weeks and then returned to Exploris and replaced with fresh individuals, this occurred a total of three times over the course of sixweeks. Tank water temperature was the same as Strangford Lough, N.I. (54.3909^{o} N, -5.57232^{0} W), ~13°C, +/- 1°C, which was the source of the sand-filtered seawater.

Adult male *Carcinus maenas* (*N* = 216, carapace width range 65-75mm) were collected along the shoreline of Strangford Lough. Crabs were sampled within a narrow size range of carapace width due to the role that size plays on predator feeding rates (Schröder *et al.*, 2016). Measuring carapace width is a widely used and robust method of sizing decapod crustaceans (e.g. Mascaró and Seed, 2001; Naczk *et al.*, 2004; Todd *et al.*, 2006; Haig *et al.*, 2016; Öndes *et al*., 2017). The crabs were maintained in three communal glass flow-through tanks (1.2m x 0.4m x 0.4m), at a density of 30 crabs per tank. These tanks were supplied with sand-filtered seawater. Crabs were fed *ad libitum* with Atlantic herring (*Clupea harengus*). Crabs were used once, and 90 fresh crabs were used every two weeks. Crabs were starved for 48 hours prior to experiments to increase hunger and reduce individual variation.

Mytilus edulis were collected near Horse Island, Kircubbin, N.I. (54.4677 N, -5.5403 W). *M edulis* were separated into adults (*N* = 600, shell length 60-70mm) and spat (7-17mm). Measuring shell length is a common and robust method for sizing bivalves (e.g. Belz *et al.*, 2010; Fitzer *et al.*, 2014; Jin *et al.*, 2012; Melzner *et al.*, 2011; Okaniwa *et al.*, 2010). *M. edulis* adults were maintained in an opaque plastic tank (80cm x 60cm x 40cm) and spat were maintained in simple plastic buckets. Tanks and buckets were supplied with sand-filtered (non-UV) seawater for the duration of the experiments.

2.3.3. Setup

The experimental design employed a tri-trophic chain with an elasmobranch (*R. clavata* or *S. stellaris)* as the top predator, crabs (*C. maenas)* as the mesopredator and mussel spat (*M. edulis)* as a basal prey species (Figure 2.1). A blank (no elasmboranch) was also used as a predator treatment control. The reef presence treatment was binary: reef present and reef absent. Each elasmobranch was used eight times for consistency and to limit the time spent at the lab i.e. to reduce unnecessary stress. One full replicate (all six treatments) was run per session (day), n = 12. Three *C. maenas* were used per experiment to account for variability in crab response. Though it is understood that a disadvantage of using multiple individuals is the potential for intraspecific interactions to occur, the likelihood of *Carcinus maenas* feeding on mussels in a solitary manner in the wild is low, and the benefits of using multiple crabs were considered to outweigh the disadvantages of individuals not feeding and skewing results. The experimental design is presented in detail in Figure 2.2.

Experimental arenas were opaque circular tanks (2.2m diameter and 0.7m depth) with a constant flow of sand-filtered seawater (see Figure 2.3). It is well understood that mussels increase byssal thread production in response to predation (Reimer and Tedengren, 1997; Brown *et al.*, 2011) in order to enhance structural refugia and reduce predation risk. However, there is evidence that byssal production alone cannot protect mussels from crab predation (Capelle *et al.*, 2016). To assess the protective effects of a mature reef structure as well as the tactile interactions between mussels and crab predators, a complex reef made of live *M. edulis* was used in my experiments. This allowed us to account for an indirect effect that cannot be assessed when using immovable false reefs; the active degradation of prey refugia by mesopredators. 'Reefs' were composed of live adult mussels (n = 100) which were allowed

to clump for 16 hours in a fixed area within the experimental arena prior to experiment start. This was achieved using a plastic pipe (internal diameter ~35cm) open at both ends. For consistency, it was ensured that no adult mussels were attached via byssal threads to any other individual before being placed into the pipe. Any individuals that were adhered to the pipe once it was removed at the start of the experiment were carefully detached.

Spat (*n* = 50) were then applied to the reef within the tube one hour prior to the start of the experiments. Any byssal threads attached to the tube at the start of the experiments were carefully detached , as with the adult mussels. The spat density was derived from the known maximum consumed by adult *C. maenas* in previous studies (Barrios-O'Neill *et al.,* 2017; Joyce *et al.,* 2019). For reef-free treatments, spat were also placed in a tube one hour prior to the commencing of the experiments, but with no reef structure. Tubes were consistently placed in the same approximate location within the arenas for all treatments, Figure 2.4 illustrates the positioning of the different components of the experiments.

A single *R. clavata* or *S. stellaris* individual was introduced immediately after the addition of the spat. After the one-hour spat clumping period, the pipe was removed and the crabs were added, signalling the start of the experiments. For consistency, the same technique was used each time to ensure the detaching of byssal threads from the interior of the pipe. This involved the gentle rotation of the pipe clockwise and then anticlockwise, followed by visual inspection (and gentle removal of any further attached individuals by repetition of this motion) before the pipe was lifted straight up and clear of the reef, as to mitigate disruption of the reef structure itself. A one-hour clumping period was chosen as it was not a prohibitively long period, but still allowed for byssal thread attachment, an obstacle crabs would face in the wild. Crabs (*n* =3) were placed directly adjacent to the reef/spat for every treatment. three

crabs were used to mitigate the impact of individual variation and they were placed adjacent to the reef to ensure consistency. Crabs and elasmobranchs were free moving with no restrictions. Each replicate lasted three hours, with the removal of the crabs signalling the end. The reef was then removed and both adult and surviving spat mussels were enumerated. In instances were adult mussels had been predated by crabs, (i.e. shells had been crushed and pulled apart), these samples were accounted for in the analysis of spat consumption. Significant dismantling of the reef by crabs was defined as ≥10 adult individuals (i.e. 10% of the reef) being removed from the main reef structure.

For the predator-free control treatments, the protocol was identical except for the exclusion of an elasmobranch. The reefs, spat and crabs were all set up and handled in the same way as in the *R. clavata* and *S. stellaris* treatments.

2.3.4. Statistical Analyses

All analyses were performed in R 4.0.3 (R Core Team, 2020). Spat consumption was recorded as count data for each treatment. Spat consumption data were found to be left skewed and zero-inflated (see Figure 2.5 For residuals). A Vuong test showed that a zero-inflated Poisson model fit the data more accurately than a standard Poisson GLM, and thus, the data were analysed using a zero-inflated Poisson GLM. Predator presence and reef presence were computed as factors with interaction. Confounding factors (i.e. the day of recording, the consumption of mature mussels and reef dismantling), were also computed as standalone factors to determine their impact on crab spat consumption. Direct comparisons between the two predator treatments with and without reef present were made using zero-inflated (following Vuong test verification) Poisson GLMs. A direct comparison of spat consumption in the presence/absence of reef in predator-free controls was performed using a standard

Poisson GLM, as a Vuong test showed no significant improvement of fit using a zero-inflated model. Analysis of mature mussel consumption by crabs was also performed using appropriate GLM models, as ascertained by Vuong tests. Kruksal-Wallis tests were used to compare reef dismantling between predator treatments.

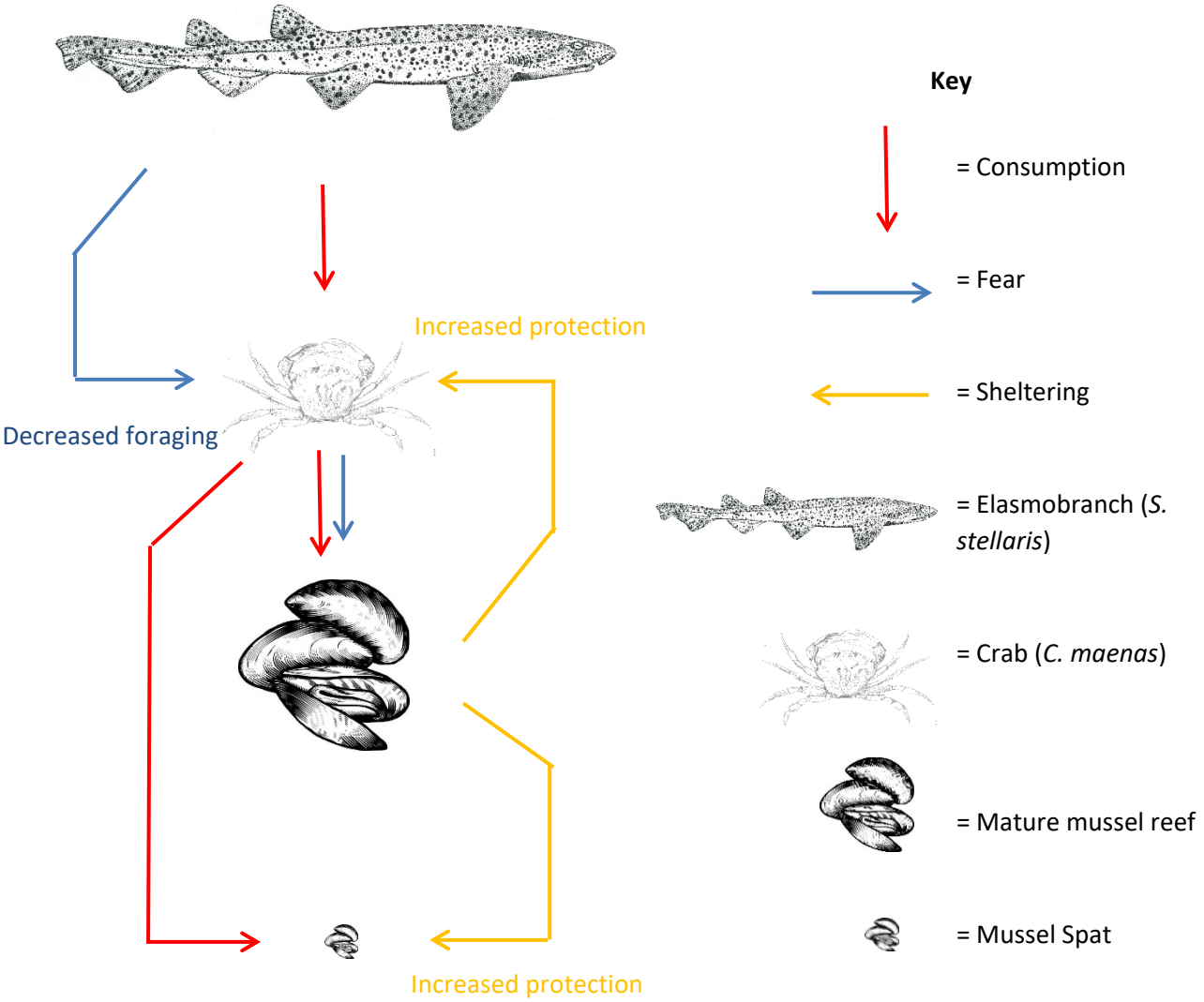

Figure 2.1 Tri-trophic chain with interactions. Both the consumptive and non-consumptive effects of each part of the tri-trophic chain are highlighted via the arrows labelled in the key. *S stellaris* image credit – Joana Parente (Parente, 2018), all other images in public domain.

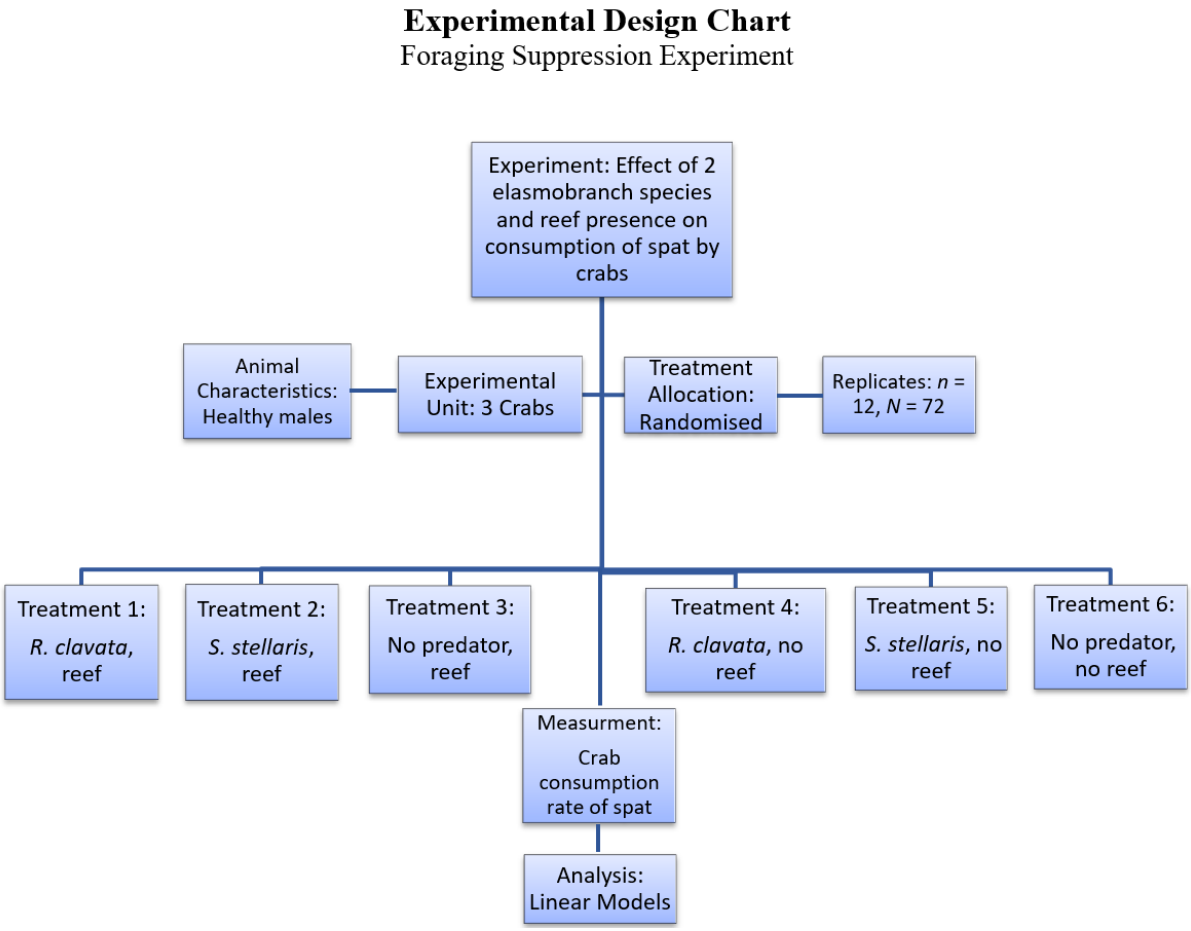

Figure 2.2 Summary flowchart of experimental design. Experimental units, treatment allocation type, animal characteristics, measurements taken, analyses chosen and individual treatment combinations are displayed.

Figure 2.3 Experimental tanks – Image showing the opaque plastic tanks used to carry out all the behavioural experiments for this study. Yellow pipes at the back of the tanks were the seawater inflow pipes and the blue pipes at the front (facing the camera) were the outflow pipes. All tanks were on a raised concrete platform to ensure that the water level in each tank was even, as the ground in this area was sloped.

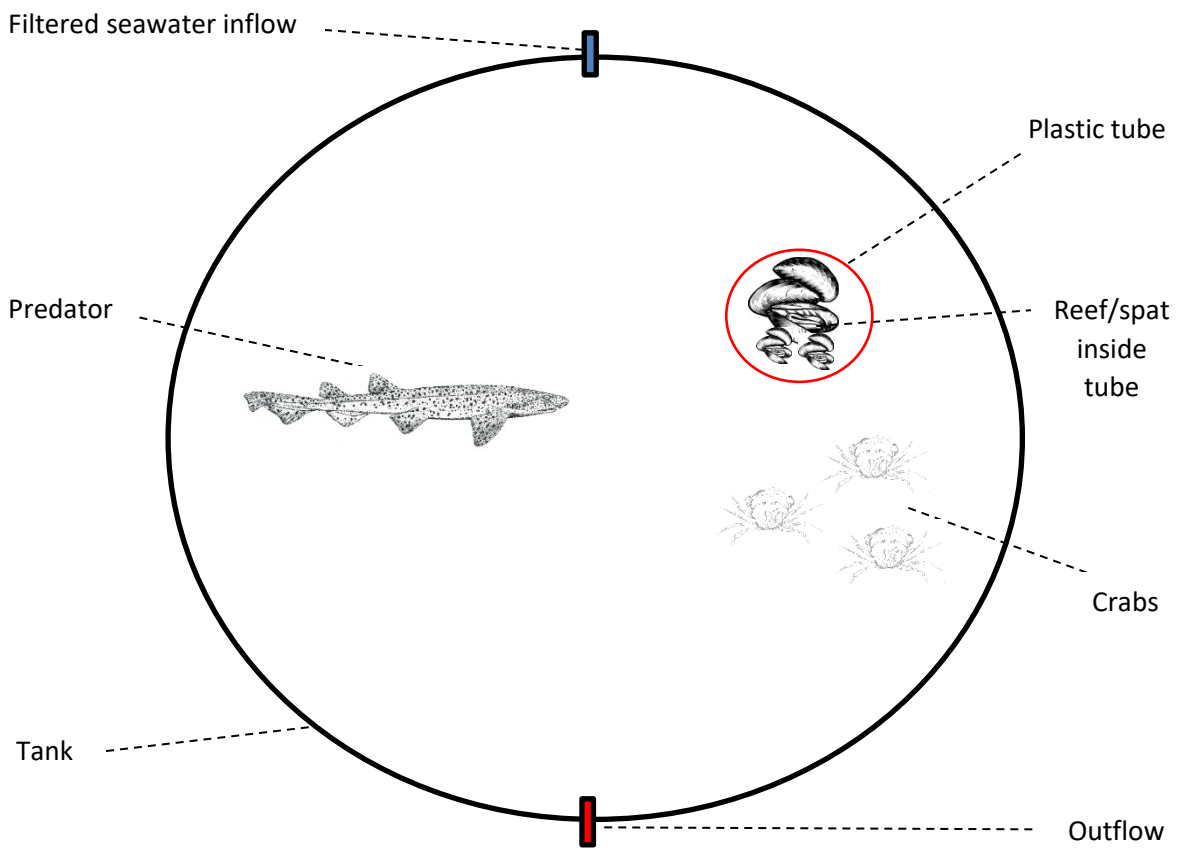

Figure 2.4 Experimental tank setup (not to scale). Reef/spat were placed near the centre right-hand side of the tank for all trials. Filtered seawater entered from the back of the tank via hose and exited at the front via an overflow pipe. Crabs were placed close to the reef at the beginning of the 3 hour experimental period.

2.4. Results

2.4.1. Spat consumption GLMs

See Table 2.1 for the descriptive statistics for spat consumption across all treatment groups. Crabs consumed significantly fewer spat in the presence of both *R. clavata* ($z_{(5,77)} = -4.475$, $p < 0.05$) and *S. stellaris* ($z_{(5,77)} = -2.959$, $p < 0.05$) compared to predator-free controls. Crabs also consumed fewer spat in the presence of mature mussel reef ($z_{(5,77)} = -6.887$, $p < 0.05$) compared to reef-free treatments. See Figure 2.5 for data residuals and spat consumption across all treatments. In instances where crabs consumed mature mussels from the reef, spat consumption was also significantly higher ($z_{(3,35)} = 4.998$, $p < 0.05$), with predator treatment having no effect on mature mussel consumption ($p > 0.05$), see Figure 2.6. There was no significant difference in crab spat consumption between the two predator treatments (all $p > 0.05$), see figure 2.7. In predator-free controls, crabs consumed fewer spat in the presence of reef compared to the absence of reef ($z_{(1,23)} = -7.33$, $p < 0.05$), see figure 2.8.

2.4.2. Reef dismantling Kruskal-Wallis

When either elasmobranch predator was present, there was no evidence of significant reef dismantling in any replicates. However, crabs dismantled the reef in 25% of the replicates in the predator-free control treatment, a difference that was statistically significant ($H_{(36)} = 1.459$, $p < 0.05$).

Table 2.1 Descriptive Statistics of spat consumption data – Showing the mean, , standard error, and standard deviation for spat consumption across all treatment groups.

		$\bar{x}$	SE	SD
R. clavata	**Reef**	1.5	0.4	1.4
	No reef	5.3	2.6	8.9
S. stellaris	**Reef**	2.3	0.9	3.1
	No reef	6.5	3.3	11.5
Control	**Reef**	5.3	1.4	4.9
	No reef	14.3	4.1	14.1

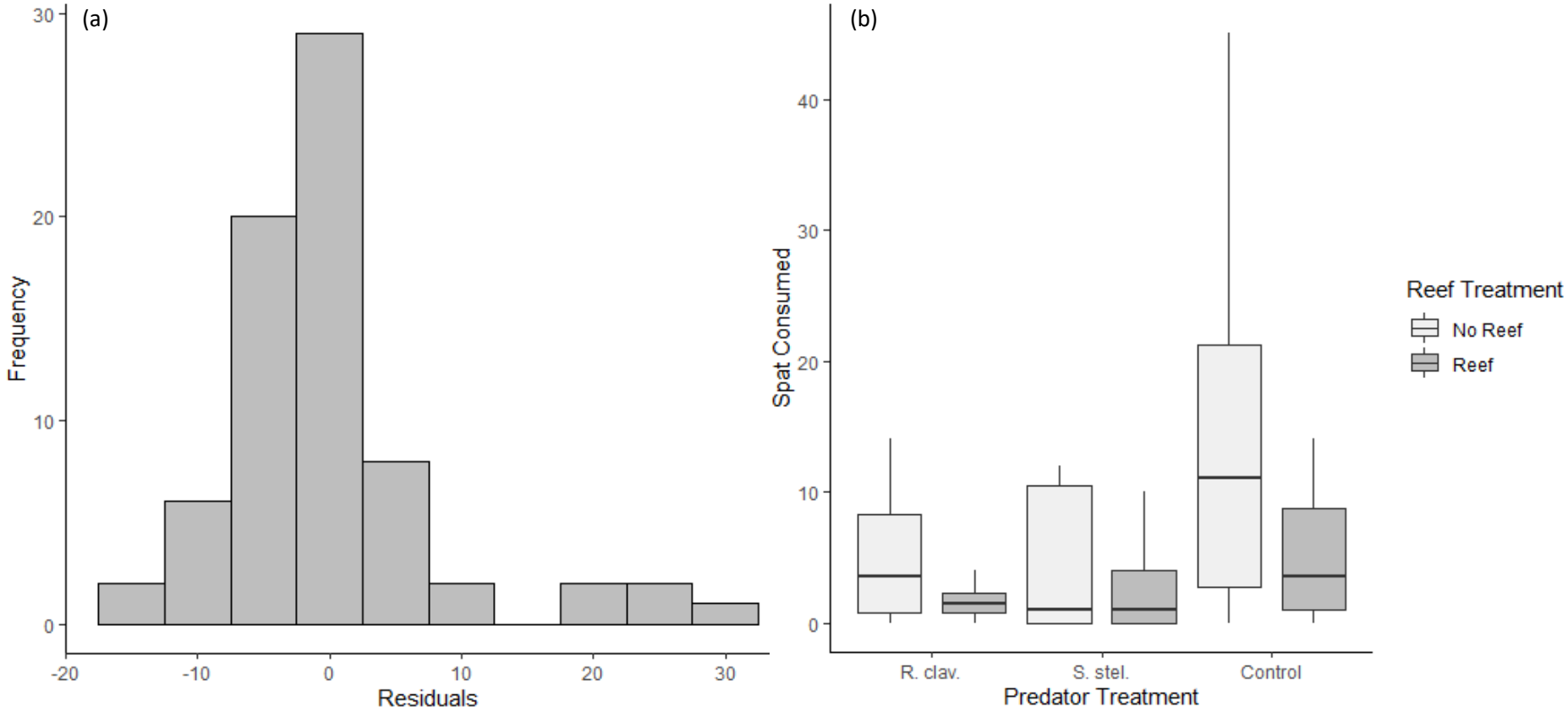

Figure 2.5 Data residuals and spat consumption across all treatments – (a) Histogram displaying the distribution of data residuals across all treatments, showing left-skew and zero- inflation (b) Boxplot of the total spat consumed per experimental unit of three *C. maenas* within the three-hour long experimental runtime. Grouped by predator presence and *M. edulis* reef presence treatments. Whiskers represent variability outside the upper and lower quartiles.

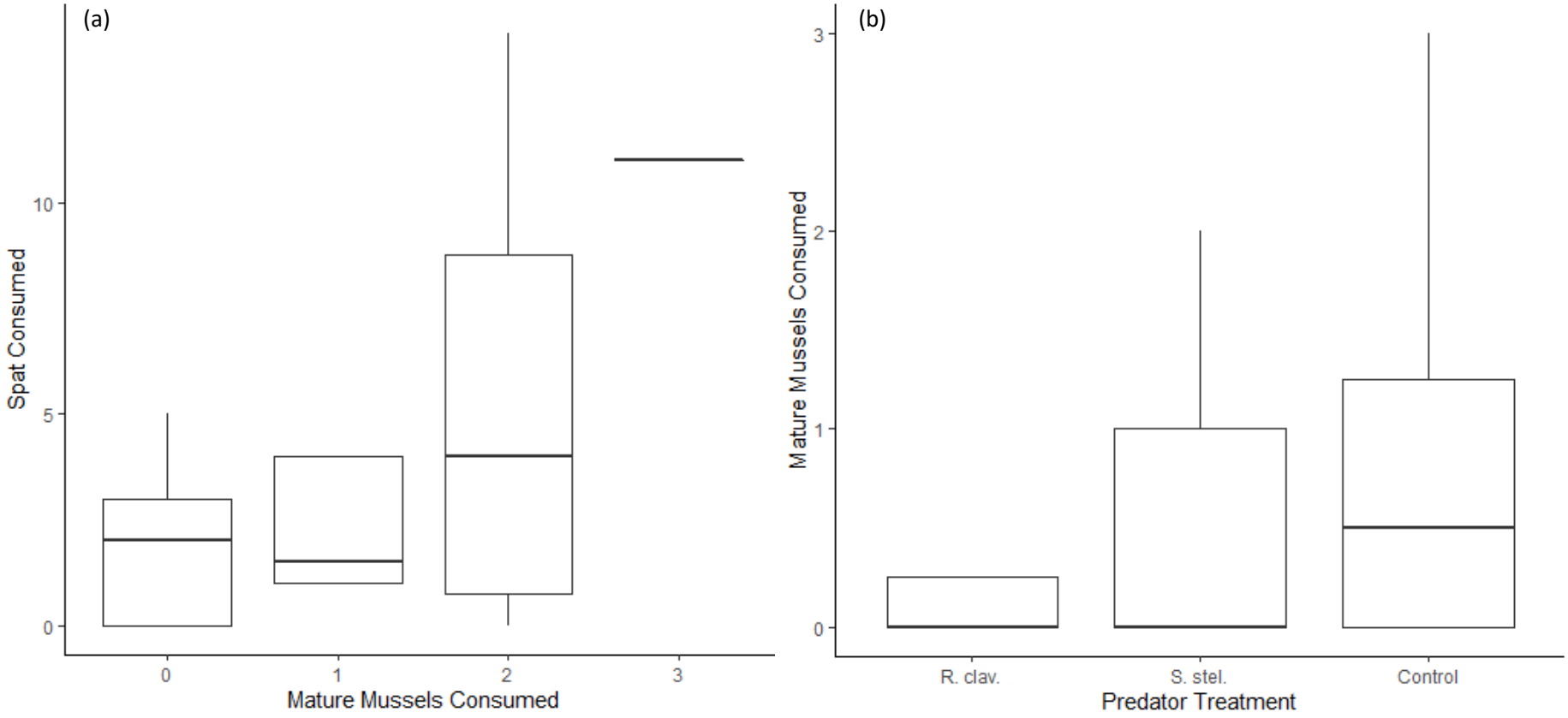

Figure 2.6 Boxplots of spat consumption and mature mussel consumption - (a) Boxplot illustrating spat consumption in relation to the number of mature mussels consumed per experimental unit of three crabs. (b) Boxplot illustrating the number of mature mussels consumed across predator treatments per experimental unit of three crabs. Whiskers in both plots represent variability outside the upper and lower quartiles. While there is a positive visual trend, no significant difference between treatments was found during analysis.

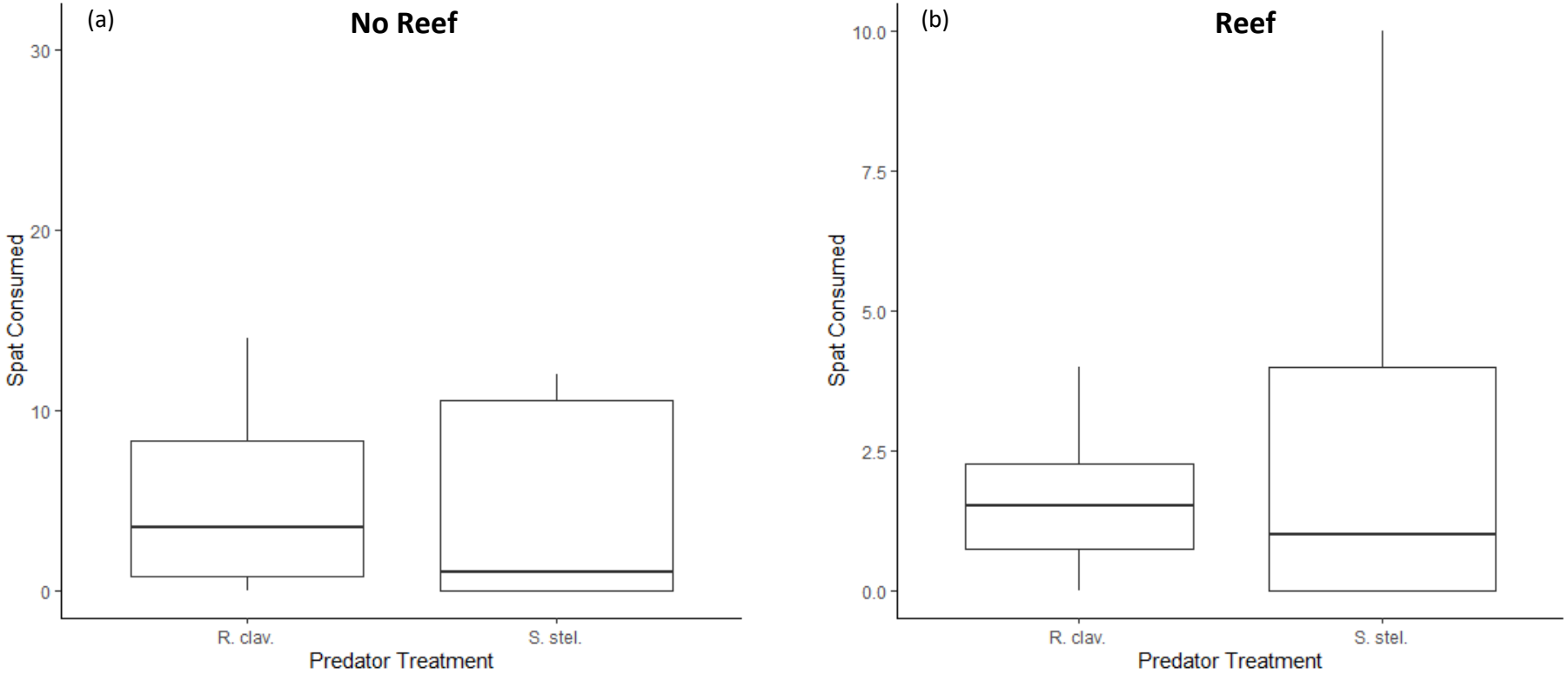

Figure 2.7 Box plots directly comparing spat consumption by *C. maenas* across predator treatments in the presence and absence of reefs. (a) displays spat consumption per experimental unit of three crabs between *R. clavata* and *S. stellaris* treatments when reef was absent. (b) displays spat consumption per experimental unit of three crabs between *R. clavata* and *S. stellaris* treatments when reef was present. Whiskers in both plots represent variability outside the upper and lower quartiles. There were no significant differences between predator treatments.

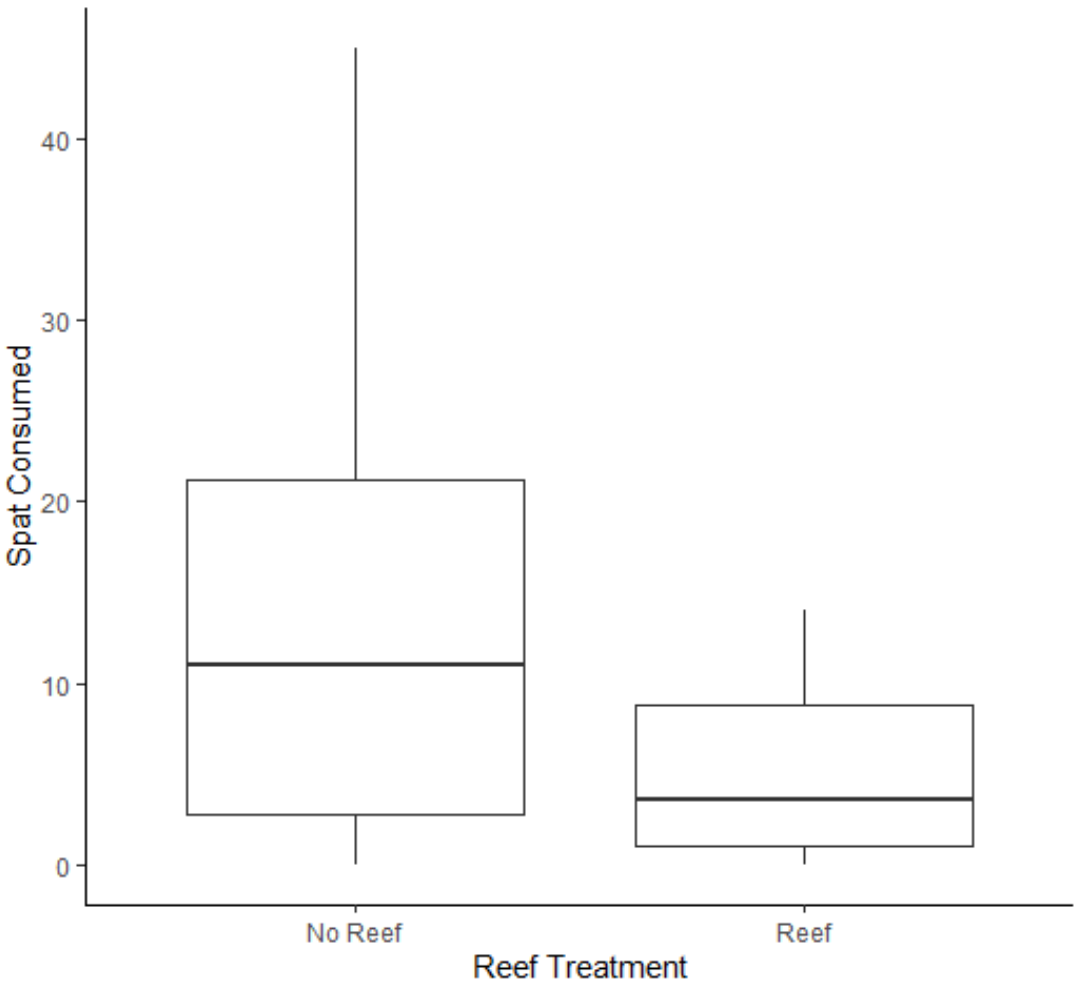

Figure 2.8 Spat consumption in the across reef treatments in predator-free controls – Boxplot showing the number of spat consumed per experimental unit of three crabs in predator-free controls. Whiskers represent variability outside the upper and lower quartiles. Significantly fewer spat were consumed by crabs when reef was present in controls.

2.5. Discussion

Here, the aim was to quantify the effects of two functionally similar elasmobranch predators on crab feeding in the presence and absence of mussel reef. The results showed that in the absence of reef, crab feeding was suppressed by both elasmobranchs and that there was no significant difference in crab feeding between predator species. When reef was present, crab feeding was reduced primarily by reef presence. When reef was present, predator presence enhanced suppression compared to predator-free treatments but had no significant effect on overall mussel consumption. Furthermore, no significant reef dismantling was observed when predators were present, but reef dismantling occurred in 25% of predator-free controls. These results supported my initial hypotheses.

2.5.1. Transient keystone predators, trophic redundancies, and ecosystem resilience

Ecosystem resilience is the ability of an ecosystem to 'absorb' disturbances and maintain critical ecological functions while undergoing changes in ecological state (Sasaki *et al.*, 2015). Both *R. clavata* and *S. stellaris* suppressed mesopredator feeding when reef was absent in my experiments, reducing the amplitude of the effect of the crab mesopredators on the mussel prey. Furthermore, these results suggested that reef presence dampened the effects of predator presence and took primacy in suppressing crab feeding. This was evidence that both *R. clavata* and *S. stellaris* could suppress mesopredators in a context-specific manner, forming a feedback loop with reef presence, (i.e. both elasmobranchs acted as transient keystone predators), consistent with previous findings using the elasmobranch *Raja microocellata* (Barrios-O'Neill *et al.*, 2017). However, my findings built on the work of Barrios O'Neill *et al.* (2017) by using larger, live reef structures and comparing two different elasmobranch predator species, which allowed for the

investigation of predator species differences/similarities and potential reef dismantling behaviours performed by crabs. This is discussed in the section '***2.5.2. Non-consumptive interactions and cascading effects***'. Other recent examples of species not typically considered keystone predators acting as transient keystone predators include otters in North America, which can enhance the resistance of kelp forests to overgrazing by predating sea urchins (Smith *et al.*, 2021). Research has shown that this otter-kelp cascade might have been precipitated by the loss of a megaherbivore, Steller's Sea Cow (*Hydrodamalis gigas*), which had significant impacts on kelp forest structure and distribution (Estes *et al.*, 2016; Bullen *et al.*, 2021), (i.e. a significant change in ecological context).

These previous findings, alongside my own, provide a mounting body of evidence emphasising the importance of transient keystone predators. The biosphere has undergone extensive defaunation throughout human history (Dirzo *et al.*, 2014; Young *et al.*, 2016), leading to what has been described as the 'trophic downgrading of planet earth' (Estes *et al.*, 2011), as top predators and megafauna have been driven to extirpation, severe population decline and extinction across the globe. As Estes *et al.* (2011) stressed, the decline of these species has shifted the ecological context in which predator-prey interactions take places, with many apex predators and megafauna being replaced by species further down the trophic hierarchy. These shifts in trophic hierarchies can lead to a ecosystems entering 'alternative stable states' (Beisner *et al.*, 2003), whereby an ecosystem reaches stability after a perturbation, but with a different set of processes, factors and/or species (Holling, 1973) than before the perturbation.

A key factor influencing alternative stable states, as Beisner *et al.* (2003) highlighted, is resilience. Ecological resilience has been defined as the amount of change needed to shift

an ecosystem from one state to another (Angeler and Allen, 2016). Previous research has shown that trophic redundancy can bolster community stability and resilience to disruption (Biggs *et al*., 2020), even reducing the likelihood of extinction cascades (Sanders *et al*., 2018) within a system. As such, trophic redundancy can be an important factor for maintaining stable ecosystem states. My results are an example of trophic (functional) redundancy, as both species of elasmobranch reduced spat consumption and reef dismantling behaviours of *C. maenas* to a similar extent. Thus, the presence of a diversity of healthy populations of transient keystone predators such as *S. stellaris* and *R. clavata* could augment ecosystem resilience and stability, to the overall benefit of ecosystem health. However, my findings are not prescriptive, and more research is needed to clarify the role these species play in a wider ecosystem context.

2.5.2. Non-consumptive interactions and cascading effects

No crabs were consumed at any point during my experiments. Hence, all of the predator effects observed can be considered non-consumptive (Hoki *et al.*, 2014). My results highlight the importance of accounting for non-consumptive interactions by demonstrating that predators can cause significant cascading effects without any direct consumption occurring. Previous research supports these findings, for example, raccoons (*Procyon lotor*) alter their foraging behaviour in response to the sound of predators, without any direct interaction, enhancing survivability of the raccoon's prey via trophic cascade (Suraci *et al.*, 2016). A similar experiment to my own, the previously mentioned Barrios O'Neill *et al.* (2017) went one step further, having a predator in the presence of a mesopredator and accounting for the effect of simulated reef structures. Still, no direct predation of the

mesopredator occurred and a trophic cascade was observed, to the benefit of mussel spat survivability.

My experiment expanded upon this previous research by comparing two elasmobranch predators and including live mature reef structures to account for any reef dismantling activity. The differences between my findings and those of Barrios O'Neill *et al.* (2017) were nuanced. While both of the elasmobranch species used here showed transient keystone effects and the formation of a feedback loop with mussel reef presence, spat mortality was substantially different. Barrios O'Neill *et al.* (2017) found an increase in spat mortality in the presence of both the simulated reef and the predator, while the results presented here showed the opposite. They also found that reef had no significant effect on mussel mortality alone, while again, the experiments performed here found the opposite. A potential reason for this difference in spat mortality is the use of a larger, live, reef structure in the current study. Previous research has shown that the brachyuran crab *Callinectes sapidus* favours feeding on the edges of bivalve reef habitat, but is less likely to do so as habitat patchiness and predation pressure increase (Macreadie *et al.*, 2012). Macredie *et al.* (2012) posited that the interior of a more continuous reef structure provided a refuge for the prey of the crab which patchy areas did not. This might explain why Barrios *et al.* (2017) found that the presence of their comparatively small patch of simulated reef (consisting of four silicone filled *Modiolus* mussel shells), had no significant protective effect by itself, but counterintuitively increased spat consumption when a predator was present, as no substantial interior refuge was present. The much larger and more complex reef used here, consisting of 100 adult *M. edulis* mussels, likely provided significantly more shelter for the mussel spat, accounting for these differences. These findings demonstrate the importance of considering the size and complexity of biogenic structures when attempting to quantify

the effects of predator-prey interactions, as the context of shelter availability and habitat continuity can influence the cascading effects of transient keystone predators on basal species.

2.5.3. Reef dismantling and consumption of mature mussels

The use of live mussel reefs in my experiments allowed for the quantification of important predator-mesopredator-basal interactions, in the form of reef dismantling and the consumption of mature mussels. My results showed that crabs did not dismantle any reef structures in the presence of either predator, but dismantled reefs in 25% on control treatment replicates. It is likely that the crabs were dismantling the reef structures to reach the spat that were hidden within the reef matrix, as it is known that crabs favour smaller mussel spat over adult mussels, most likely to reduce wear to their chelae (Kamermans *et al.*, 2009; Smallegange and Van Der Meer, 2003). A thorough examination of the scientific literature did not yield another study that experimentally recorded this dismantling behaviour, and while the threat fear-released mesopredators pose to bivalve reefs has been recognised, previous studies have focused on mussel recruit mortality and crab preferences for smaller prey (Bleile and Thieltges, 2021; Capelle *et al.*, 2016; Christie *et al.*, 2020; O'Connor *et al*., 2013; Prado *et al.*, 2020).

As such, my experiments have quantified a crab foraging behaviour that has not yet been experimentally addressed, the impacts of which could have significant ecological consequences relating to the fragmentation of biogenic reef habitats. For example, increased reef patchiness can compound mesopredator predation on specific basal species, such as scallops (MacReadie *et al.*, 2011), altering reef community dynamics. The suppression of this dismantling behaviour by elasmobranch predators, as observed in the

current study, is an example of the vital ecosystem services provided by transient keystone predators.

Chapter 3

Are Brachyuran Mesopredators with Overlapping Ecological Niches Suppressed Homogeneously by Predation Risk?

Impact Statement

The experimental design, setup and data collection for this chapter was performed over a highly time-suppressed period due to the loss of other work due to COVID-19 restrictions. Furthermore, video trawl data provided by AFBI was analysed to determine benthic mesopredator densities for a chapter of my thesis that became untenable due to COVID-19 restrictions. That data analysis informed this chapter, as *Liocarcinus depurator* was found to be the most abundant mesopredator observed in the video trawls, thus I chose to include *L. depurator* species in my experimental design.

3.1. Abstract

Species respond heterogeneously to predation risk and this variation should be considered when investigating predator-prey interactions. Species-specific differences in anti-predator response are an understudied aspect of predator-prey interactions. Quantifying mesopredator anti-predator response effects can enhance the scientific understanding of the ecosystem services provided by predators. Brachyuran crabs are common mesopredators in marine ecosystems. Here, the presence of the elasmobranch *Raja clavata*, a known predator of brachyurans, was used to measure differences in feeding response in three crab species within a trophic guild (the common shore crab, *Carcinus maenas,* the sandy swimming crab *Liocarcinus depurator* and the velvet swimming crab *Necora puber*). All three species were observed to decrease feeding in the presence of the predator. However, *L. depurator* feeding was suppressed to a greater extent than *C. maneas* and *N. puber. N. puber* feeding was also supressed to a lesser extent than *C. maenas*. This evidence supports the hypothesis that brachyuran crabs within guilds can be suppressed in the same direction by the presence of a predator, but that they will exhibit distinct species-specific responses. Additionally, no crabs were consumed by *R. clavata* at any point, meaning these effects were entirely non-consumptive, highlighting the importance and power of the non-consumptive effects of predator presence (i.e. fear of predation).

3.2. Introduction

3.2.1. Predation risk and variation in anti-predator response within trophic guilds

A trophic guild can be defined as a group of species that exploit the same resources in a similar manner (*sensu* Simberloff and Dayan, 1991). Guilds can be identified by behaviours such as resource partitioning (e.g. Varghese *et al.*, 2014; Rhoades *et al.*, 2018). Resource partitioning can, in turn, be influenced by predation risk (e.g. Naman *et al.*, 2019), with predators further up a trophic hierarchy heterogeneously altering the foraging behaviour and resource use of their prey (Sivy *et al.*, 2018).

A key factor in these predator-prey interactions is diversity of anti-predator response. Organisms can show diversity in anti-predator behaviour (Magurran *et al.*, 1993). For example, teleost fish do not react homogenously to the presence of a potential predator, with some species relying on refugia more often than others and some choosing to move less and switch habitat use, enhancing predator avoidance and shelter use (Hölker *et al*., 2007; Lehtiniemi, 2005). Such changes in anti-predator response can lead to variation in resource use across multiple species (e.g. Sharma and Borgstrøm, 2008), altering community structure across (Klages et al., 2014) and within (Arribas *et al.*, 2018) guilds. As such, variation in anti-predator response an important factor affecting ecosystem functioning. Thus, when investigating predator-prey interactions, variation in anti-predator should be accounted for, as it can affect prey spatial use, foraging behaviour and refugia use, all of which are key components in what is known as a 'Landscape of Fear' (Laundré *et al.*, 2010; Bleicher, 2017).

A landscape of fear can be defined as the variation in predation risk experienced by an animal while inhabiting it's environment (Laundré *et al.*, 2010), including fluctuations in features such

as habitat availability/complexity and predator presence/abundance. A previous review of landscape of fear research stressed that prey perception of predation risk should be considered the defining measure of a landscape of fear (Gaynor *et al.*, 2019). Prey perception and the cost of prey anti-predator response were integral components to the framework described in the Gaynor *et al.* (2019) review, and this informed the current study.

Another example of landscape of fear research by Bleicher (2017), emphasised the need for research to consider 'convergent species from similar environments', as it is less studied than other factors influencing the landscapes of fear experienced by animals. There are examples of terrestrial birds (Fernández-Juricic *et al.*, 2004), freshwater teleosts (Voellmy *et al.*, 2014) and amphibians (Arribas *et al.,* 2018) displaying substantial variation in anti-predator response within guilds, but marine examples in the scientific literature are currently lacking. Previous studies have also discussed this gap in scientific knowledge, such as Frid *et al.* (2012), which identified that the differences and/or similarities between sympatric species in their boldness or aversion to predation risk when acquiring resources is less well studied than other aspects of predator-prey interactions, especially in the marine environment. Thus, quantifying the variation in anti-predator response between members of a marine mesopredator guild was the purpose of the current study.

3.2.2. Aims and objectives

The study aimed to quantify the variation in feeding across three members of a brachyuran trophic guild in response to predation risk. The objective was to record the number of *M. edulis* spat (post-juvenile) consumed by *L. depurator*, *N. puber* and *C. maenas* when the elasmobranch predator *R. clavata* was present and absent. The number of spat consumed within three hours was used as the metric for these experiments. This allowed for the

quantification of variation in feeding suppression effects by *R. clavata* between the crab species.

3.2.3. Hypotheses

It was hypothesised that predator presence would decrease the feeding rate across the trophic guild, but that crab intensity of anti-predator response (reduction in feeding) would vary between species. This hypothesis was based on findings from previous research that showed that different brachyuran crab species display nuances in their feeding behaviour (ap Rheinallt, 1986; Sponaugle and Lawton, 1990; Lee and Seed, 1992) and in their aggressive/defensive behaviour(Silva *et al.,* 2010; AFBI, 2015).

3.3. Methods

3.3.1. Species Chosen

The representatives of a mesopredator trophic guild for the current study were the brachyuran crabs *Carcinus maenas*, *Liocarcinus depurator* and *Necora puber*. These species inhabit trophic levels ranging from 2.6 to 3.5 (Ansell *et al.*, 1999; Careddu *et al.*, 2017; Freire and Gonzalez Gurriaran, 1995; Schaal *et al.*, 2010). These species were identified as being members of a trophic guild as they have overlapping distributions (Amaral *et al.*, 2009; Hill, 2008; Wilson, 2008) and display resource portioning in shared habitats (Griffin *et al.*, 2008). *C. maenas* is predominately intertidal, while the other two species are predominately subtidal There are also morphological differences between the species, such as *N. puber* having more robust chelipeds than that of *L. depurator* (Freire *et al.*, 1996) to accommodate the more intermediate prey it prefers to feed on. *L. depurator* also grows to a smaller maximum carapace width of ~50mm (Hill, 2008), compared to the maximum carapace width of >80mm observed for *N. puber* (Wilson, 2008). These nuances in biology suggest, that while these species are members of a trophic guild, it should not be assumed that they will respond homogenously to predators.

All of the crab species used in this chapter of the thesis were known to feed upon mussels (ap Rheinallt, 1986; Calderwood *et al.*, 2015; Capelle *et al.*, 2016; Freire and Gonzalez Gurriaran, 1995; Smallegange and Van Der Meer, 2003). *C. maenas* in particular heavily predate mussels and favour smaller individuals (Smallegange and Van Der Meer, 2003). Mussel spat were chosen for the current study, over other prey shared by the crab species chosen, because mussels can act as ecosystem engineers by forming biogenic reef structures,

increasing habitat complexity (Commito and Rusignuolo, 2000). This provides ecosystem services in the form of habitat enhancement and shelter for ecologically and commercially important species (Kent *et al.*, 2016; Kristensen *et al.*, 2015). As such, determining the heterogeneity of indirect benefits for bivalves caused by the suppression of brachyuran mesopredators has implications for ecosystem resilience and recovery research. The blue mussel, *Mytilus edulis*, is a biogenic reef forming mussel that can be found in subtidal and intertidal habitats (Saier, 2002) that the 3 crab species also inhabit. Furthermore, *M. edulis* is known to enhance habitat complexity and biodiversity (Norling and Kautsky, 2007) to the benefit of many associated species. This made *M. edulis* an appropriate prey species for the current study.

The skate species *Raja clavata* was chosen as the predator species for the tri-trophic chain used here. *R. clavata* was chosen as its diet includes up to ~50% brachyura (Barría *et al.*, 2015), making it a crab predator, and it inhabits a trophic level of 3.8 ± 0.2 (Palomare and Sa-a, 2008), greater than that of the crabs chosen, thus making it an appropriate model predator for the current study.

3.3.2. Animal collection and husbandry

Experimental stock of *R. clavata* (*n* = 4, length = 70-80cm) were obtained from the local Exploris aquarium in Portaferry, Northern Ireland. Stocks of healthy male *Carcinus maenas* (*n* = 40, carapace width 50-60mm; *n* = 40, carapace width 70-80mm), *Liocarcinus depurator* (*n* = 40, carapace width 50-60mm) and *Necora puber* (*n* = 40, carapace width 70-80mm) were collected in the locality of Strangford Lough, Northern Ireland. Local pot fishermen were employed in the collection of *L. depurator* and *N. puber*, while *C. maenas* were collected by hand and via baited pots placed on the shore. *Mytilus edulis* spat (*n* = 1200) were collected in

the locality of Strangford Lough and sorted into size classes, 10-15mm shell length was used for the experiments.

R. clavata were maintained individually in 2.2m x 1.3m x 1m flow-through, sand-filtered seawater tanks at the QUB Marine Laboratory, Portaferry, Northern Ireland, prior to experiments. All skate were fed *ad libitum* on Atlantic herring (*Clupea harengus*). Any food not consumed by skate within 24 hours was removed to maintain water quality. Based on guidelines from the Elasmobranch Husbandry Manual II (Smith *et al.*, 2017), skate tanks were enriched with sand, rocks and seaweed to reduce stress. Furthermore, *R. clavata* were fed via a combination of techniques, both allowing food to fall to the bottom of the tank for foraging enrichment and via 'litter picker' style pole feeders to guarantee consumption.

The 3 crab species were maintained separately in flow-through tanks (80cm x 60cm x 40cm) at a density of 40 crabs per tank on mesocosm tables at the QUB Marine Laboratory. All crabs were fed *ad libitum* on Atlantic herring and any food not consumed within 24 hours was removed to maintain water quality. Crabs were placed into another tank and starved for 48 hours before experiments to enhance hunger. *M. edulis* spat were maintained in buckets with flow-through, sand-filtered, seawater on mesocosm tables with no additional feeding.

3.3.3. Setup

Experiments were designed as tri-trophic chains (see Figure 3.1 for illustration of the tri-trophic chains), consisting of a predator (*R. clavata*), a mesopredator (the three crab species) and prey (*M. edulis* spat). Multiple comparisons were made from these tri-trophic chain experiments. The first compared the spat consumption of size-matched (50-60mm) *L. depurator* and *C. maenas* in the presence and absence of *R. clavata*. The second compared

the spat consumption of size matched (70-80mm) *N. puber* and *C. maenas* in the presence and absence of *R. clavata*. The third compared the spat consumption of the two *C. maenas* size classes (to determine effects of size class) and the last compared *L. depurator* and *N. puber*.

The experiments consisted of eight treatments: *L. depurator*/*N. puber* with and without skate present and 2 size classes of *C. maenas* with and without skate present. A total of 20 replicates per treatment were run, for 160 total observations. See Figure 3.2 for a summary of this experimental design. Previous research (Barrios-O'Neill et al., 2017) found that spat survivability in crab-free controls was 100% and that skate did not consume mussel spat during experiments. This evidence was supported by dietary analyses of *R. clavata* (Morato et al., 2003; Šantić et al., 2012). As such, predator-free controls were deemed redundant for this study.

Crabs were sampled within narrow size ranges by measuring carapace width to mitigate the effects of size variation, as consumer size affects feeding rates (Schröder et al., 2016) and can alter antipredator response. Measuring the carapace width of crabs was a robust method of sizing decapod crustaceans (e.g. Mascaró and Seed, 2001; Naczk et al., 2004; Todd et al., 2006; Haig et al., 2016; Öndes et al., 2017). *M. edulis* spat were sampled within narrow shell length size ranges, a common method for sizing bivalves (e.g. Belz et al., 2010; Okaniwa et al., 2010; Melzner et al., 2011; Jin et al., 2012; Fitzer et al., 2014). *R. clavata* individuals were also sampled within a tight size range, as there is evidence that crabs have the ability to assess predator body size (Hill and Weissburg, 2014).

Each *R. clavata* was deployed in experiments 20 times, each crab was used only once, and *M. edulis* spat were replaced as they were consumed. For all treatments, a single crab and 40 *M.*

edulis spat were used. The spat density was derived from the known maximum consumed by adult *C. maenas* in previous studies (Barrios-O'Neill et al., 2017; Joyce et al., 2019). In particular, Barrios-O'Neill *et al.* (2017) had a similar setup to the current study, using a *Rajidae* predator and *C. maenas*, making it useful for deriving an accurate maximum consumption rate for the crabs used in the current study. All experiments took place at the QUB Marine Laboratory in Portaferry, N.I., in three circular opaque plastic arenas (2.2m diameter and 0.7m depth), with a constant flow of sand-filtered seawater (as in Chapter 2 of this thesis).

Trials lasted 3 hours and were carried out during daylight (8am – 6pm). While *C. maenas* are known to display circatidal rhythms of behaviour (Hunter and Naylor, 1993; Lynch and Rochete, 2007), there is evidence that such behaviours are controlled by specific environmental cues, focused around salinity, temperature and pressure (Warman and Naylor, 1995). As such, my experimental setup attempted to use almost identical conditions for each experimental arena, to mitigate the potential effects of cricatidal rhythms.

Skate were placed in the experimental arenas first, followed immediately by 40 spat and then the crabs. The addition of the crabs marked the beginning of the 3-hour experimental period. Mussel spat were placed in the same approximate location in each arena and crabs were placed directly beside the spat (see Figure 3.3 for illustration of experimental setup). Both skate and crabs were free moving with no restrictions and there were no shelters provided. At the end of the 3-hour period, crabs were removed immediately to halt consumption and stop the experiment. The surviving spat were then counted. The experimental arenas were drained regularly and brushed to aid in visually identifying spat when collecting at the end of each experiment and to prevent the build-up of shell debris.

3.3.4. Statistical analyses

Spat consumption was recorded as count data for all treatments. All analyses were performed using the R 4.0.3 (R Core Team, 2020). Data were independent and as such, comparisons were made between multiple treatment combinations: *C. maenas* x *L. depurator*; *C. maenas* x *N. puber.* Count data were examined and found to follow a Poisson distribution, with left skew, due to zero-inflation, in all cases. Vuong tests confirmed that zero-inflated Poisson models fit the data more accurately than Poisson GLMs and thus, zero-inflated Poisson models were chosen to analyse the data in all cases. The confounding factor of day of recording was also computed.

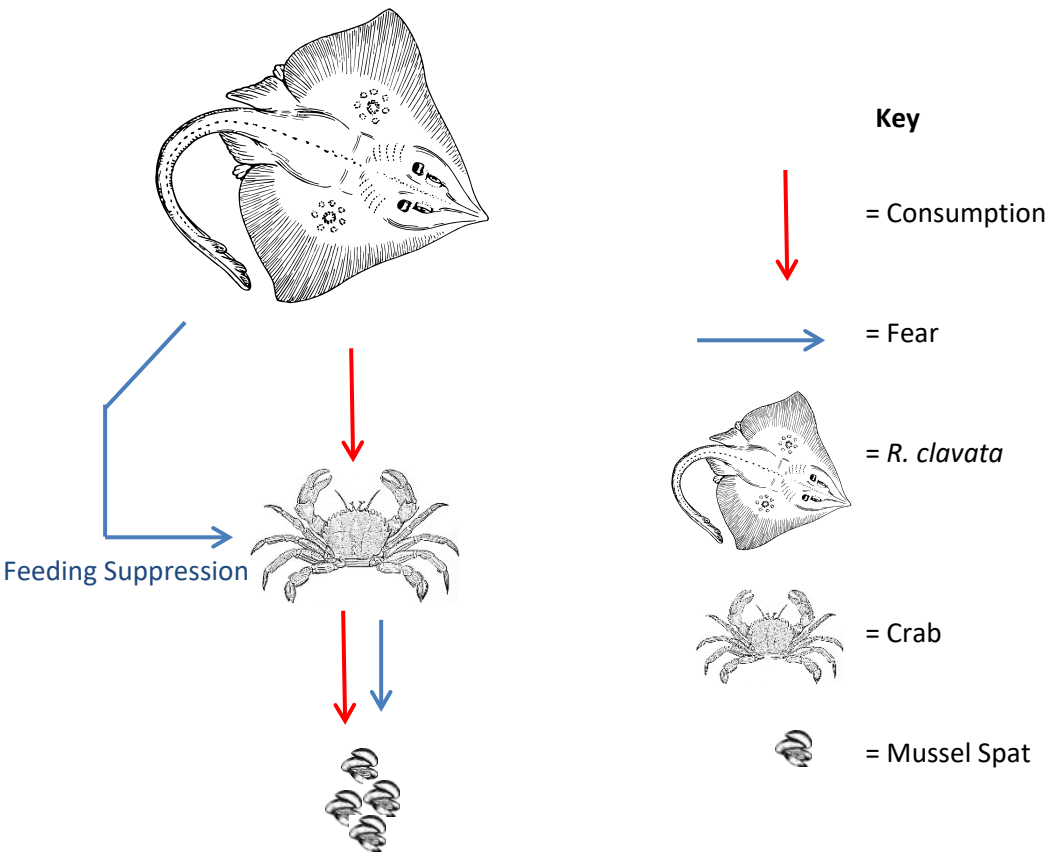

Figure 3.1 Tri-trophic chain with interactions. Both the consumptive and non-consumptive effects of the tri-trophic chain are highlighted via the arrows labelled in the key. All images in public domain.

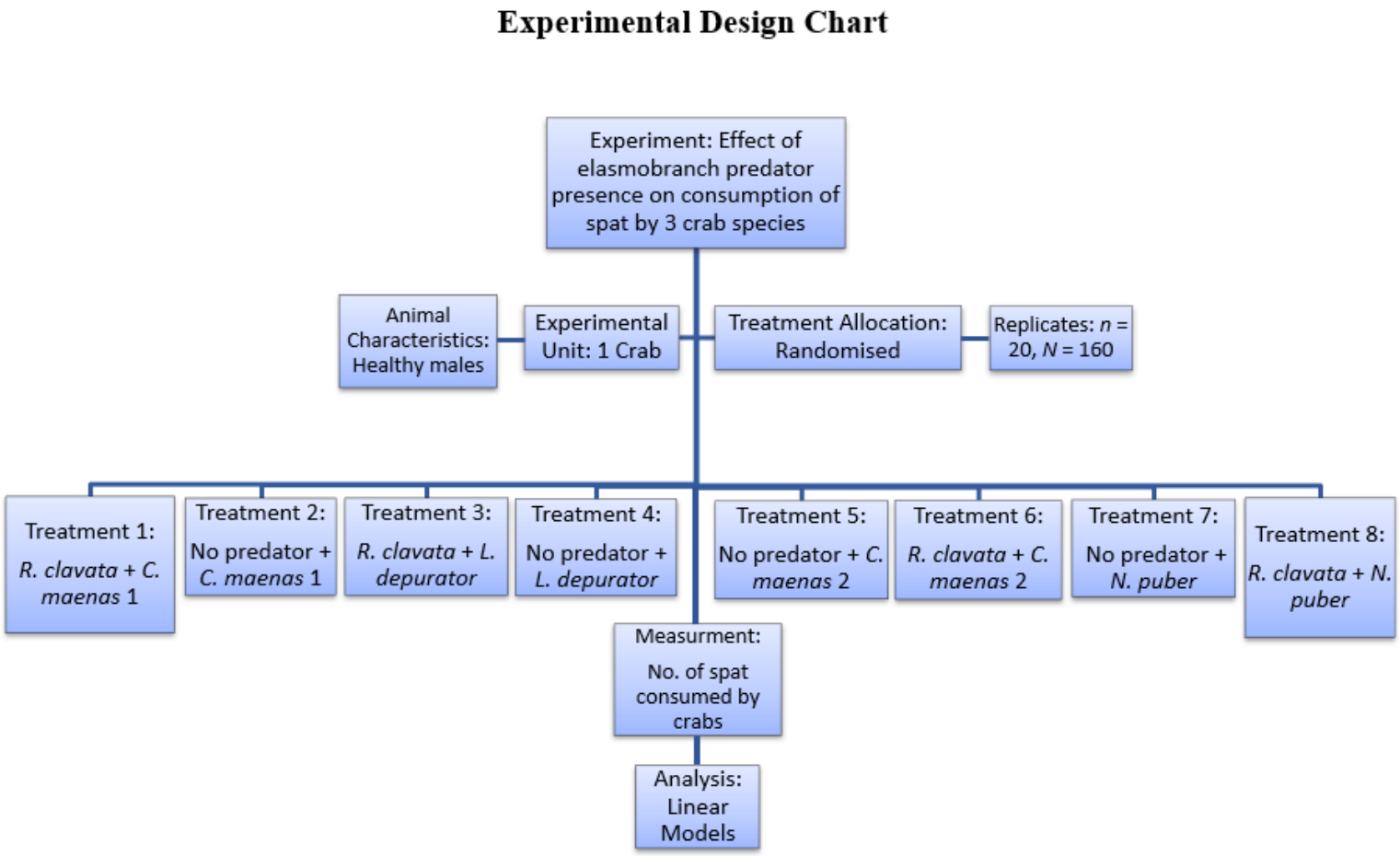

Figure 3.2 Summary flowchart of experimental design. Experimental units, treatment allocation type, animal characteristics, measurements taken, analyses chosen, and individual treatment combinations are displayed.

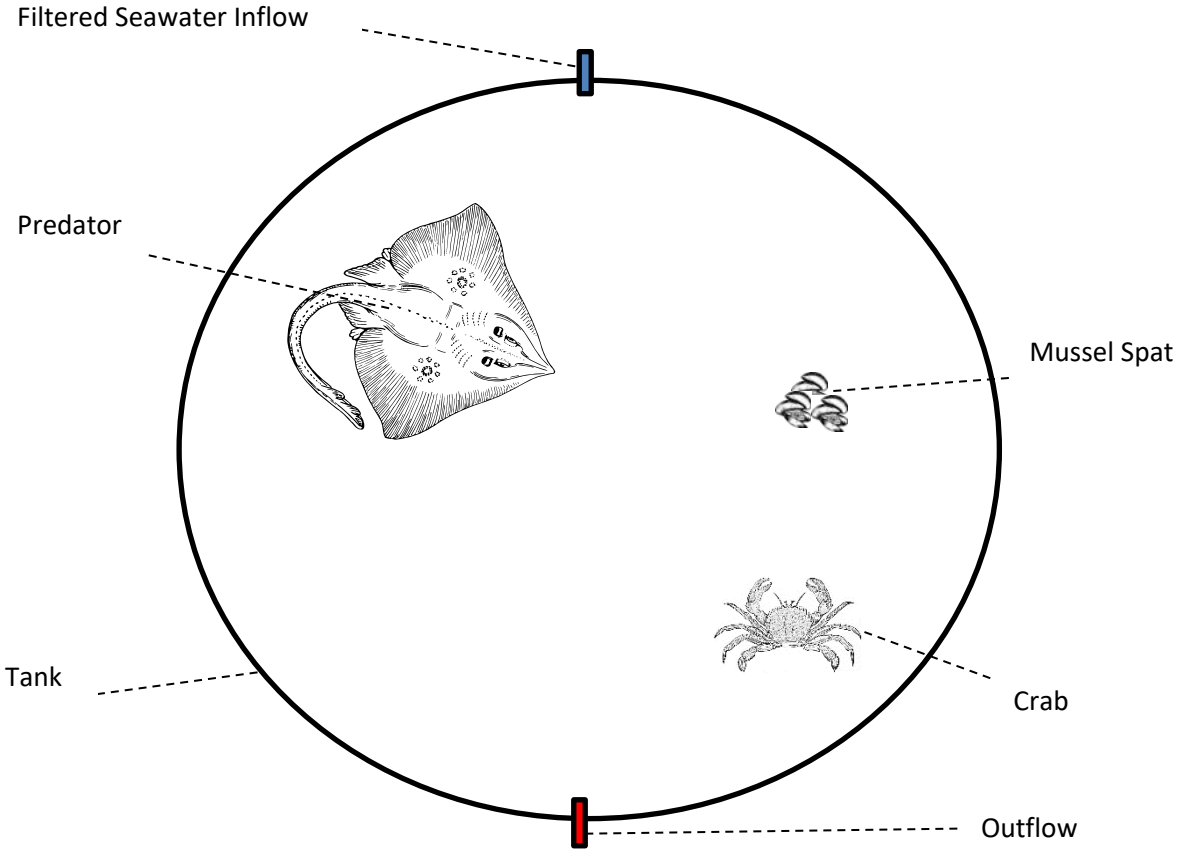

Figure 3.3 Experimental tank setup (not to scale). Spat were placed near the centre right-hand side of the tank for all trials. Filtered seawater entered from the back of the tank via hose and exited at the front via an overflow pipe. Crabs were placed close to the spat at the beginning of the 3 hour experimental period.

3.4. Results

3.4.1. L. depurator vs C. maenas

Zero-Inflated Poisson GLM

See Table 3.1 for a summary of descriptive statistics and see Figure 3.4 for data residuals, showing left-skew and zero-inflation of the data. The zero-inflated Poisson analysis showed that both crab species consumed less spat in the presence of *R. clavata* ($z_{(3,79)} = -8.048$, $p < 0.05$), and that *L. depurator* crabs consumed significantly fewer spat than *C. maenas* crabs ($z_{(3,79)} = -3.730$, $p < 0.05$). Predator presence decreased *L. depurator* spat consumption to a greater extent than *C. maenas* ($z_{(3,79)} = 3.369$, $p < 0.05$). See Figure 3.5 for illustration of spat consumption across all treatments. No crabs were consumed by *R. clavata* during any experiment. Day of recording had no significant effect on spat consumption ($p > 0.05$).

Table 3.1 Descriptive statistics of spat consumption data. Showing the mean, standard error, and standard deviation for spat consumption across treatment groups.

		$\bar{x}$	SE	SD
C. maenas	**No predator**	13.5	2.6	11.6
	Predator	2.6	0.8	3.4
L. depurator	**No predator**	8.3	2.6	11.8
	Predator	3.3	1.5	6.9

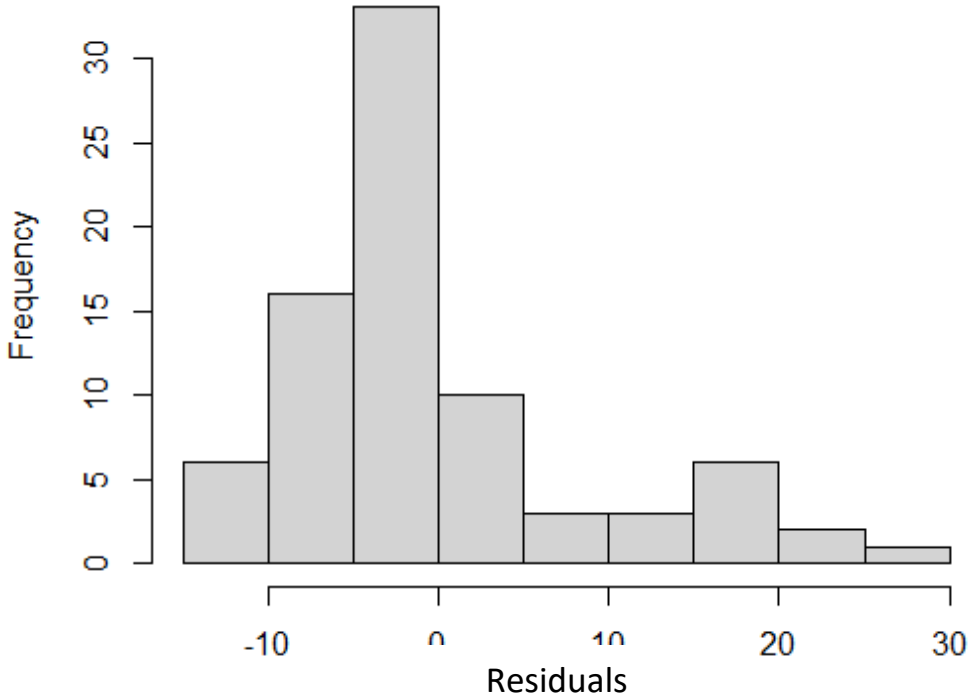

Figure 3.4 Histogram of residuals for spat consumption data for *L. depurator* vs *C. maenas*- showing left-skew and zero-inflation.

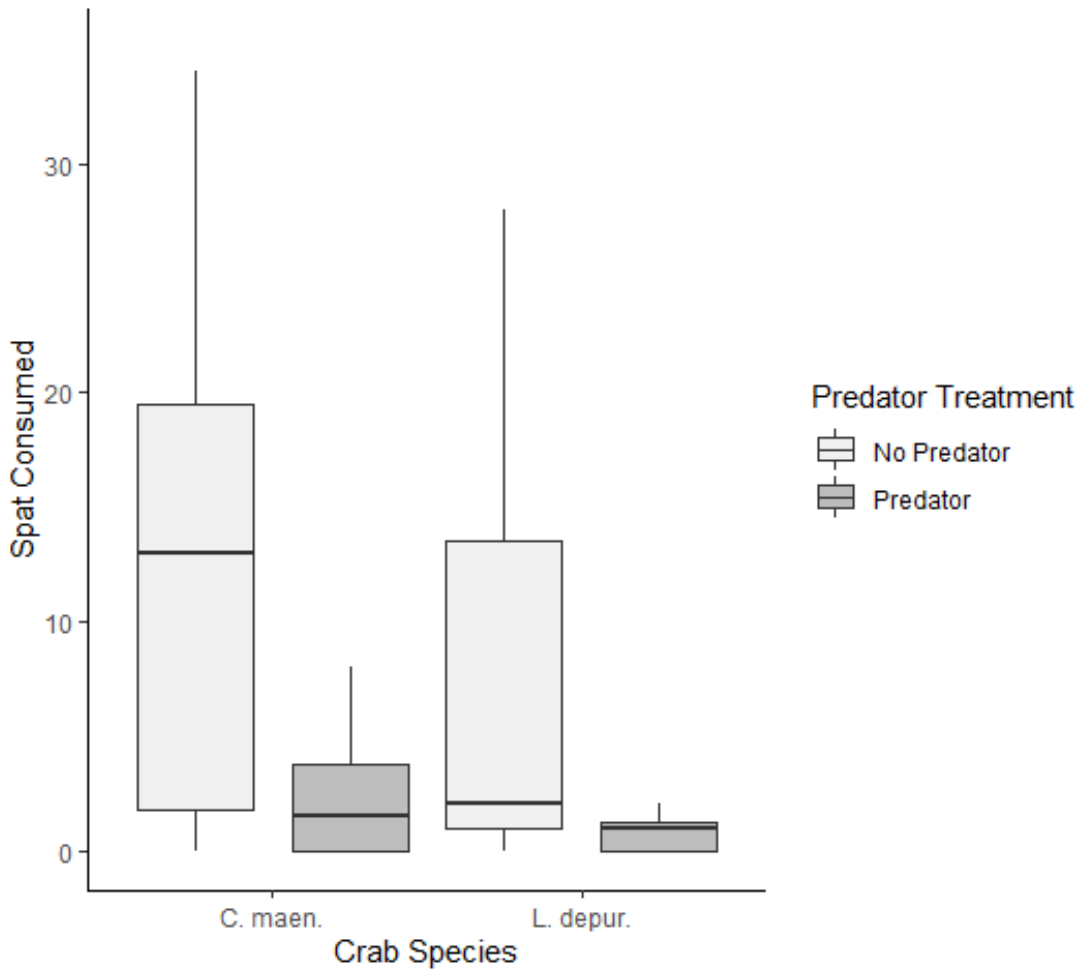

Figure 3.5 Spat consumption across all treatment combinations.. Whiskers represent variability outside the upper and lower quartiles. Crab species are displayed on the x-axis, predator treatments are indicated by shading (see legend) and the number of spat consumed within the three-hour experimental runtime is displayed on the y-axis. Central horizontal lines represent medians.

3.4.2. N.puber vs C. maenas

Zero-Inflated Poisson GLM

See Table 3.2 for a summary of descriptive statistics and see Figure 3.6 for data residuals. The zero-inflated Poisson analysis showed that spat consumption by both species was significantly lower when *R. clavata* was present ($z_{(3,79)}$ = -7.218, $p < 0.05$). *N. puber* crabs consumed significantly more spat than *C. maenas* ($z_{(3,79)}$ = 3.903, $p < 0.05$). See Figure 3.7 for illustration of spat consumption across all treatments. Predator presence decreased *N. puber* spat consumption to a lesser extent than *C. maenas* ($z_{(3,79)}$ = 2.409, $p < 0.05$). No crabs were consumed by *R. clavata* during any experiment. Day of recording had no significant effect on spat consumption ($p > 0.05$).

Table 3.2 Descriptive statistics of spat consumption data. Showing the mean, , standard error, and standard deviation for spat consumption across treatment groups.

		$\bar{x}$	SE	SD
C. maenas	**No predator**	11.8	2.2	9.7
	Predator	2.6	0.8	3.7
N. puber	**No predator**	14.7	2.9	13.2
	Predator	7.8	2.3	10.4

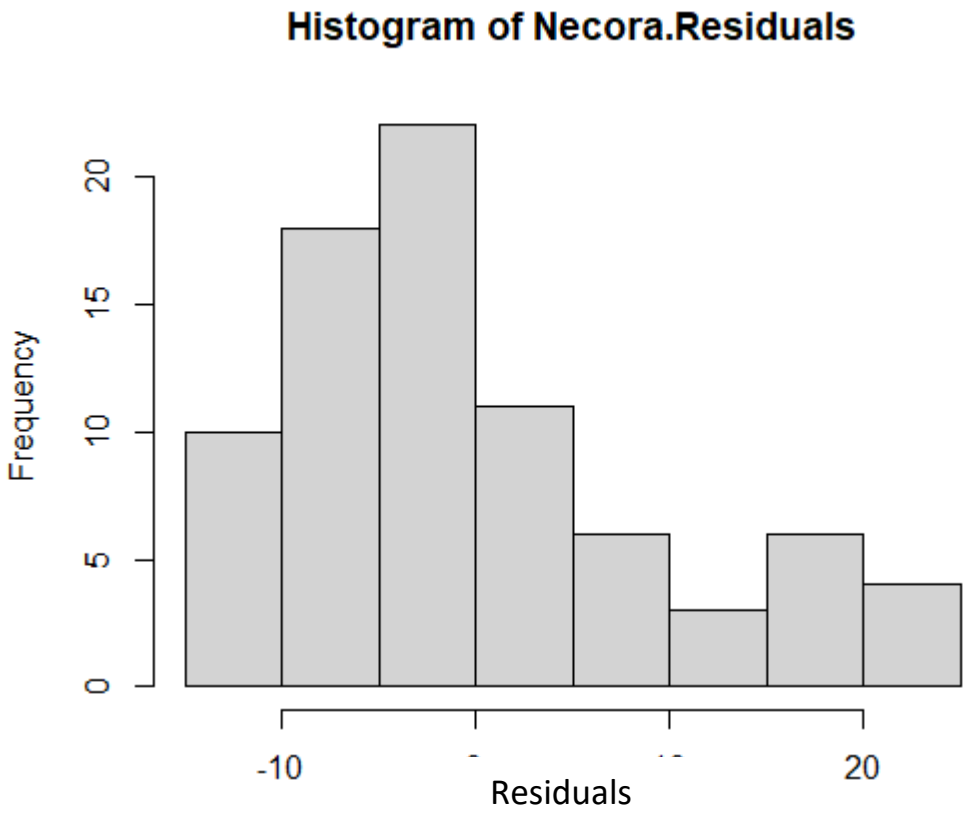

Figure 3.6 Histogram of residuals for spat consumption data for *N. puber* vs *C. maenas*– showing left-skew and zero-inflation.

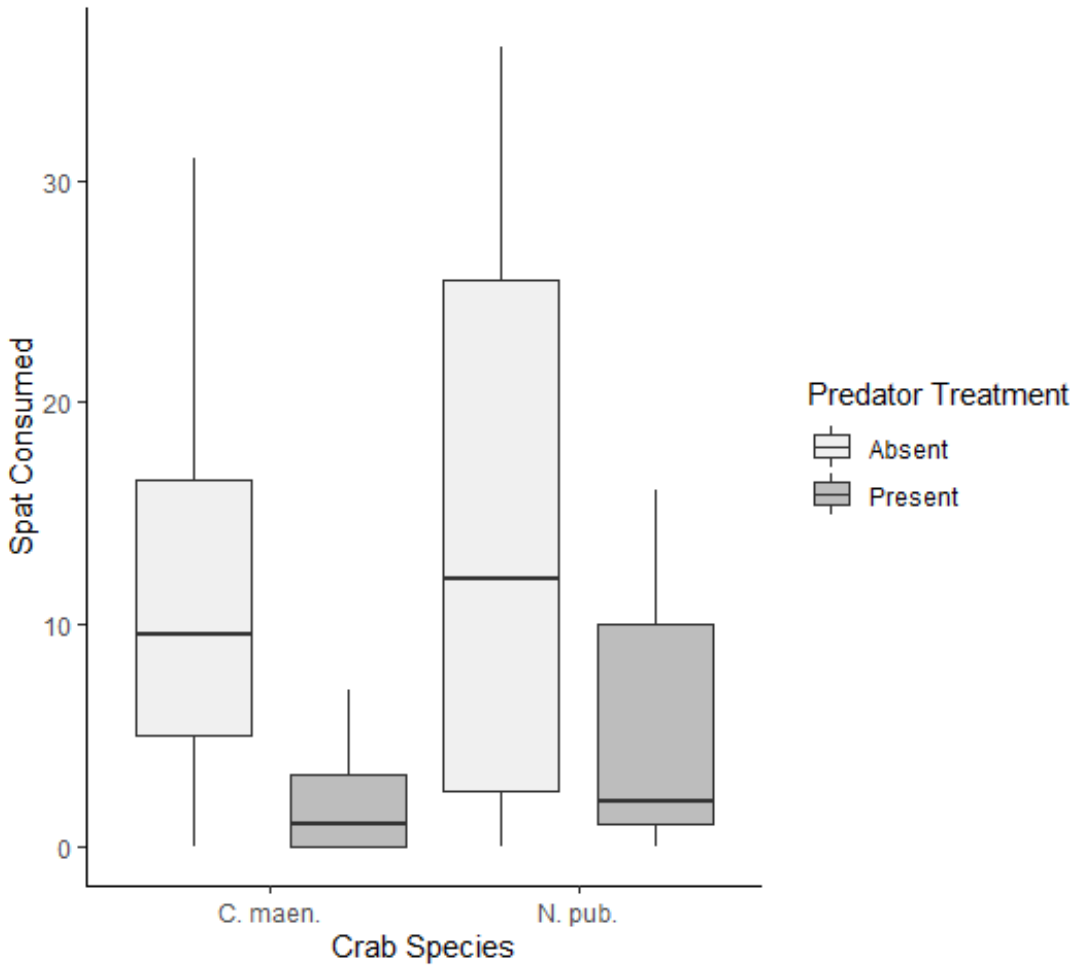

Figure 3.7 Spat consumption across all treatment combinations. . Whiskers represent variability outside the upper and lower quartiles. Crab species are indicated on the x-axis, predator treatments are indicated by colour (see legend) and the number of spat consumed within the three-hour experimental runtime is displayed on the y-axis. Central horizontal lines represent medians

3.4.3. L. depurator vs N. puber

3.4.3.1. Zero-inflated Poisson GLM

See Table 3.3 for a summary of these statistics and see Figure 3.8 for data residuals. Zero-inflated Poisson analysis showed that *N. puber* consumed more spat than *L. depurator* when *R. clavata* was present ($z_{(1,39)}$ = -2.285, $p < 0.05$). There was no difference in significant difference in consumption between the species when *R. clavata* was absent ($p > 0.05$), see Figure 3.9 for illustration of these data. Day of recording had no significant effect on spat consumption ($p > 0.05$).

Table 3.3 Descriptive statistics of spat consumption data. Showing the mean, standard error, and standard deviation for spat consumption across treatment groups.

		$\bar{x}$	SE	SD
N. puber	**No predator**	14.7	2.9	13.2
	Predator	7.8	2.3	10.4
L. depurator	**No predator**	8.3	2.6	11.8
	Predator	3.3	1.5	6.9

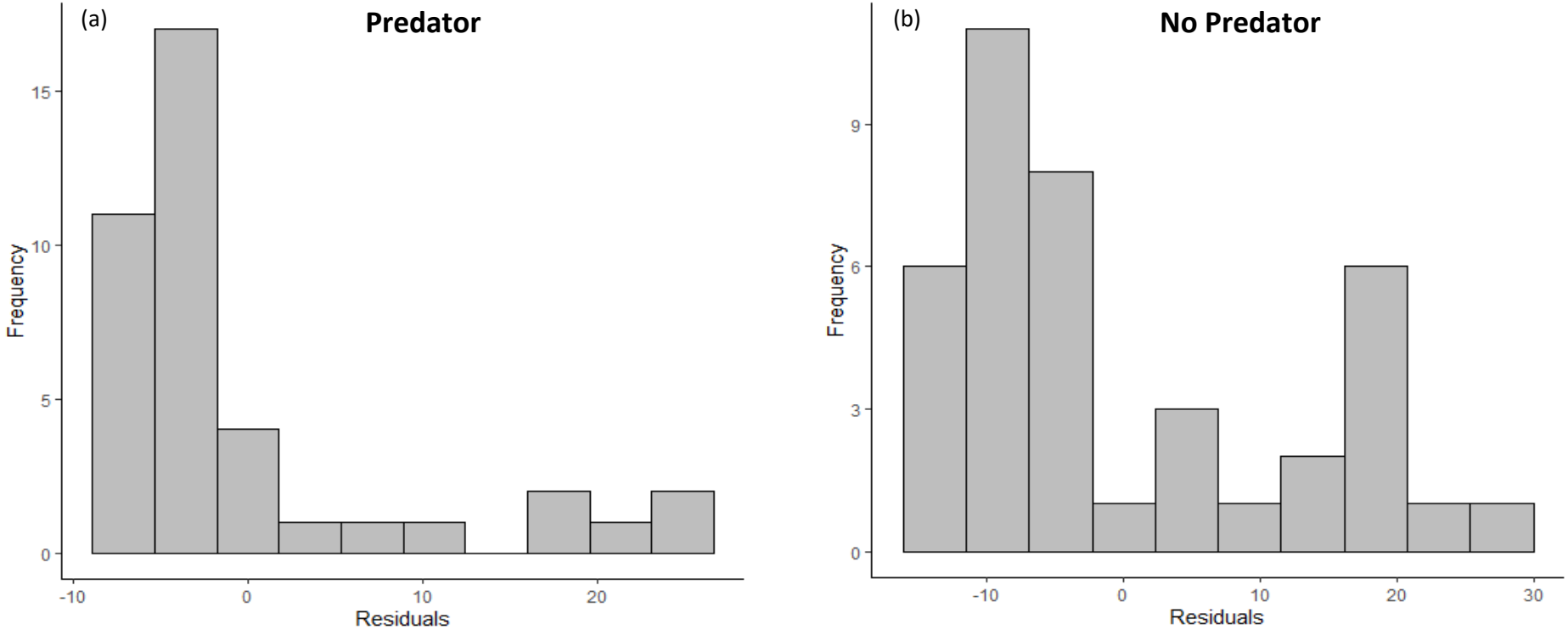

Figure 3.8 Residual data for spat consumption of *N. puber* and *L. depurator*. (a) displays data residuals of for treatments with *R. clavata* present, (b) displays data residuals for treatments with *R. clavata* absent. Both distributions were left-skewed and zero-inflated.

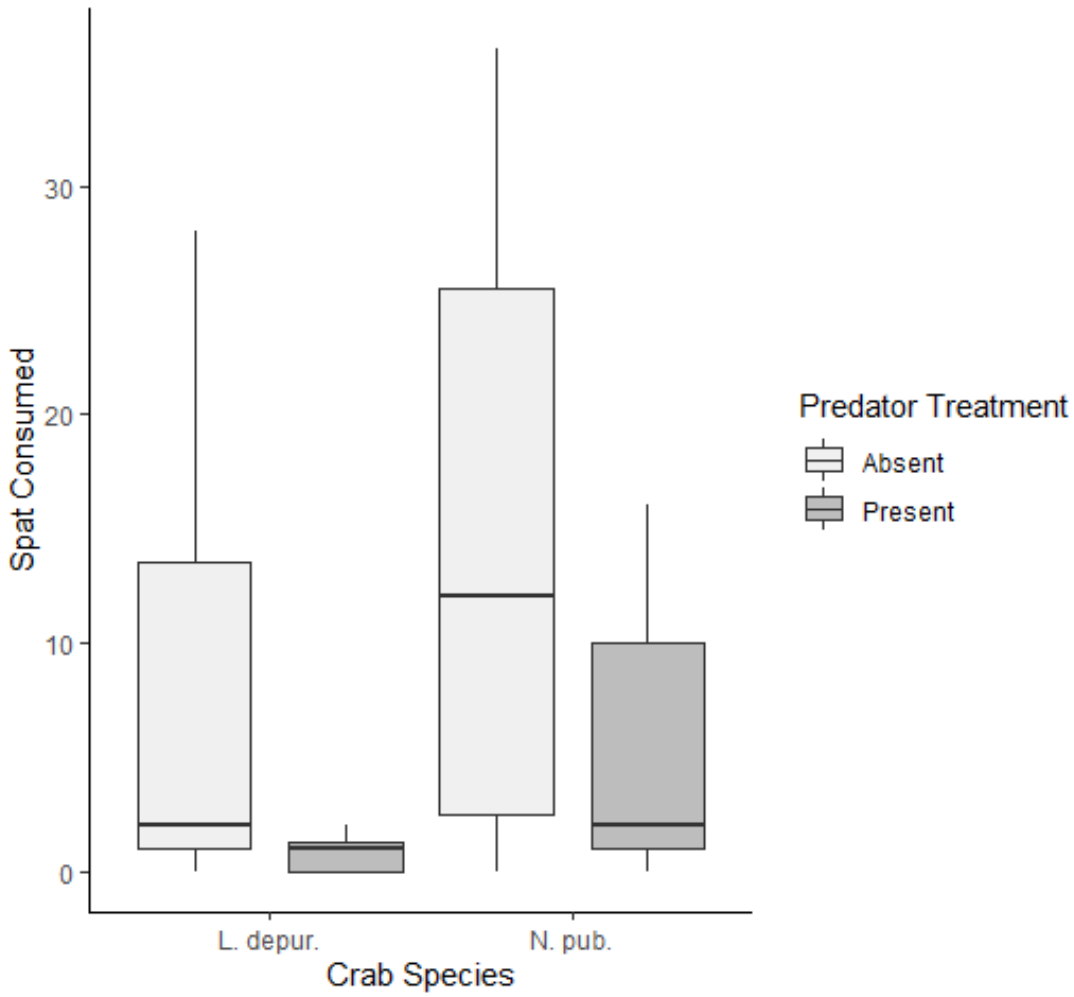

Figure 3.9. Spat consumption across treatment combinations. Whiskers represent variability outside the upper and lower quartiles. Crab species are indicated on the x-axis, predator treatments are indicated by colour (see legend) and the number of spat consumed within the three-hour experimental runtime is displayed on the y-axis. Central horizontal lines represent medians

3.5. Discussion

This study investigated whether the presence of a potential predator would consistently suppress feeding across three members of a mesopredator trophic guild. The results showed that all three guild members had lower spat consumption in the presence of *R. clavata*, but there were nuances in their response to predator presence. Additionally, no crabs were consumed by *R. clavata* at any point, highlighting these effects as non-consumptive. These results supported the hypothesis that predator presence supresses feeding across multiple mesopredator species within a guild, but to different intensities based on species-specific anti-predator response.

3.5.1. Implications – Biodiversity, community structure and ecosystem functioning

The findings of the current study provided further evidence that there is significant behavioural aspect to community structure and functioning, mediated by predator-prey interactions and that functionally similar species may not react homogenously to predator presence. Previous research has found, that perceived predation risk can alter the structure of communities (Hua *et al.*, 2013), and this process can be mediated by behavioural responses to predation (Hammill *et al.*, 2015). Furthermore, predators have been shown to suppress the 'overall amounts of primary producers consumed' while having specific effects on individual feeding rates (Catano *et al.*, 2016).

As Catano *et al.* (2016) stressed, the suppression provided by predators is important for ecosystem functioning, as predators can maintain a 'reefscape of fear', whereby changes in prey feeding patterns in response to predation risk can enhance the heterogeneity in resource distribution and exploitation. The changes in resource distribution and exploitation caused by

prey response to predation risk are important, as increased spatial resource heterogeneity can enhance the positive effects that diversity can have on ecosystem functioning (Tylianakis *et al.*, 2008). Moreover, changes in resource heterogeneity, as mediated by predators, have been identified as 'an integral part of natural ecological systems' (McIntosh *et al.*, 2004). Thus, the results presented here, in the context of this previous research, suggest that marine predators such as *R. clavata* could enhance ecosystem functioning by causing guilds of mesopredators to have similar, but nuanced, anti-predator responses that can differentially alter basal species survivability and increase resource heterogeneity.

3.5.2. Implications - Mesopredator suppression and cascading benefits

These findings are of particular relevance in instances where predators may be utilized for the provision of ecosystem services such as mesopredator suppression or the triggering of beneficial trophic cascades. The results of the current study showed that the presence of a predator suppressed the feeding of multiple species across a mesopredator guild, precipitating a trophic cascade. In turn, this improved the survivability of a basal ecosystem engineer species (*M. edulis*). *M. edulis* has be identified as an ecosystem engineer species as it is known to enhance habitat complexity and facilitate ecosystem functioning, to the benefit of a myriad of other species (Norling and Kautsky, 2007). Recent research has shown that a significant threat to *M. edulis* is predation of recruits (spat) by mesopredators such as *C. maenas*, amongst others (Christie *et al.*, 2020). One of the likely contributing factors to an increase in mesopredator predation, as identified by Christie *et al.* (2020), was the overfishing of top predators in the area, indicating a potential case of mesopredator release.

Mesopredator release refers to the releasing of mesopredators from predation pressure (Prugh et al., 2009). Mesopredator release occurs when one or more predator species is

perturbed or extirpated from an ecosystem, for example the removal of sharks from a marine ecosystem can release their prey from fear and intimidation (Frid *et al*., 2008). In turn, the extirpation of predators typically leads to an increase in the abundance of the released mesopredator and changes in mesopredator behaviour, causing cascading effects throughout the trophic hierarchy, known as 'trophic cascades' (Myers *et al*., 2007). In relation to the findings of the current thesis chapter, although there were variations in the intensity of mesopredator suppression observed in this study, all the mesopredator species were suppressed to the benefit of *M. edulis* spat. As such, the results presented here highlight a ecosystem service provided by elasmobranch predators such as *R. clavata*, that of mesopredator suppression across guilds, which could buffer ecosystems against the negative impacts of mesopredator release and enhance recovery efforts related to degraded biogenic reef habitats.

3.5.3. Implications – Modelling ecosystem interactions and between-guild predation

The results presented here demonstrated that different mesopredator guild members can react to a predator in the same way , in that they all reduced their feeding as a form of anti-predator response, but with varying intensities. These findings contribute to a growing number of studies that suggest that ecosystem models based on 'model' organisms, or oversimplified, single-species experiments should be viewed with great caution, as the effects of specific species may not be universal. For example, extensive research into multiple predator effects or 'MPEs' has shown that, for more accurate assessments of predator-prey interactions, multiple predator species should be considered (Sih *et al.*, 1998; Sokol-Hessner and Schmitz, 2002; Griffen, 2006; Van Son and Thiel, 2006; Atwood *et al.*, 2009).

Chapter 4

Fear Released Species and the Trophic and Non-trophic Factors Affecting Feeding Success Between Conspecifics

Statement of collaboration

This chapter was carried out in collaboration with another researcher, the now Dr James Dickey, who was a PhD student at the time of data collection and initial draft writing. The design, data collection and initial draft of this chapter were performed in collaboration with Dr Dickey. Other than retaining three figures, and two equations and their associated explanations from initial collaborative drafts, this text is entirely my own the work has undergone substantial changes. I recognise the valued input and assistance from Dr Dickey in the realisation of this chapter.

4.1. Abstract

Some invasive species can be considered 'fear-released' as the systems they invade are host to few, if any, natural enemies. As such, techniques commonly applied in invasive species research can provide valuable insight into the effects of fear-released species on ecosystems. Here, functional response and interaction scoring techniques were used to quantify the effects of conspecific presence, prey density and spatial availability on the feeding success of the crab *Carcinus meanas* on mussel spat (*Mytilus edulis*). Specific treatments used clay discs to mimic conspecific presence allowing the calculation of predicted functional responses and interaction scores in the absence of conspecific interactions. The treatments used were [1x crab], [2x crab], [3x crab], [1x crab + 1x disc], [1x crab + 2x discs]. These techniques allowed for quantification of the effects of conspecific interactions versus the effects of the reduction in spatial availability caused by conspecific presence. *C. maenas* displayed destabilising 'Type II' functional responses across all predicted and observed treatments. Proportional spat consumption was decreased by an increase in conspecific density ($p < 0.05$) and prey density ($p < 0.05$). At lower conspecific density (two crabs), feeding synergy significantly increased with increasing prey density, but there was no difference between crab treatment groups, suggesting prey density was the primary factor affecting conspecific interactions at low crab densities, making them less antagonistic. Conversely, at higher conspecific density (three crabs), there were no significant difference between prey densities, but an increase in conspecific density significantly decreased feeding synergy, making interactions more antagonistic. These results suggested that higher densities of conspecifics can affect feeding success not simply by reducing spatial availability (density mediation), but by increasing antagonistic interaction between individuals (trait mediation).

4.2. Introduction

4.2.1. Intraspecific competition and trophic vs non-trophic factors

Intraspecific competition for limited resources is a driving force for the alteration of animal behaviour and feeding strategies (Svanbäck and Bolnick, 2005; Evangelista *et al.*, 2014; Ratcliffe *et al.*, 2018). As well as affecting feeding strategies and resource availability (trophic interactions), intraspecific competition can also impact non-trophic interactions, such as spatial distribution and spatial availability. For example, intense intraspecific competition can decrease reef fish abundance in degraded coral reef habitats (Boström-einarsson *et al.*, 2013) and has been shown to alter spatial use in wolves (Rich *et al.*, 2012) and striped mice (*Rhabdomys pumilio*) (Schradin *et al.*, 2010).

Trophic factors, such as prey density, and non-trophic factors, such as habitat availability, can both shape ecological communities by altering factors including co-existence (van Veen *et al.*, 2005), habitat use and prey preference (Trussell *et al.,* 2006b). As such, quantifying the impacts of both trophic and non-trophic interactions is important for enhancing the scientific understanding of intraspecific competition and its impact on predator-prey dynamics. Disentangling the trophic and non-trophic impacts of intraspecific competition can allow for a better understanding of the underlying mechanisms driving changes predator-prey interactions.

4.2.2. Fear release, invasive species and species chosen

When an invasive species first enters a new ecosystem, they potentially have few immediate natural enemies to contend with, however, this is not always the case and even when natural enemies are present, a buffer against invasion is not guaranteed (Colautti *et al.*, 2004; Sih *et*

al., 2010). In instances where natural enemies, such as native predators, can enhance ecosystem resilience to invasion, the decline in these predator populations has been shown to exacerbate the negative impacts of invasion (Short *et al.*, 2002; Wallach *et al.*, 2010). In instances where invasive species are limited by the presence of native predators/natural enemies, they can be considered 'fear-released' in the absence or decline of these natural enemies, a phenomenon that can lead to cascading effects throughout trophic hierarchies (Frid *et al.*, 2008; Suraci *et al.*, 2016).

Changes in the feeding ecology of fear-released mesopredators can cause negative cascading effects such as habitat degradation, especially in systems with biogenic ecosystem engineer species such as mussels and oysters (Plass-Johnson *et al.*, 2010; Macreadie *et al.*, 2012; Carroll *et al*., 2015; Kulp and Peterson, 2016). The effects of fear-released species have been observed at a global scale, leading to the 'trophic downgrading of planet earth' (Estes *et al.*, 2011), to the detriment of biodiversity, ecosystem functioning and stability. Thus, improving the scientific understanding of the factors influencing mesopredator feeding is useful for informing biodiversity conservation.

Defaunation in the world's oceans (McCauley *et al.*, 2015) has led to the trophic downgrading of ecosystems (Estes *et al.*, 2011). Important marine predators such as elasmobranchs are being extirpated due to overfishing and habitat degradation (Robbins *et al.*, 2006; Ferretti *et al.,* 2010; Worm *et al.,* 2013; Pacoureau *et al.*, 2021). This removal and displacement of ocean predators has led to marine mesopredator species being released from the fear of predation, which can alter ecosystem functioning and have cascading negative effects (Ritchie and Johnson, 2009; Sieben *et al.*, 2011; del Mar Palacios *et al.*, 2016), though marine mesopredator release research is lacking in comparison to terrestrial research. There is

evidence that the brachyuran crab *Carcinus maenas* is undergoing fear-release within its native range, (Infantes *et al.*, 2016; Rudnicki, 2018; Christie *et al.*, 2020) and thus, *C. maenas* was chosen to represent a fear-released mesopredator species my study.

4.2.3. Functional responses and methods chosen

When investigating the effects of trophic and non-trophic interactions on the feeding ecology of fear-released species, insights from invasion science can be of great use. Of particular relevance is the recently recommended use of functional response (FR) to assess multiple predator effects (MPEs) (Wasserman *et al.*, 2016). Functional responses (FRs) are divided into three major 'types', Type I, Type II, and Type III. The type of functional response is determined by the relationship between the proportion of prey eaten and prey density and is calculated using logistic regression, examining different linear coefficients (*sensu* Wasserman *et al.*, 2016). The three major types of functional response are shown in Figure 4.1.

Type I responses are observed when consumption and prey density have a directly linear relationship. In the wild, these responses are generally limited to animals such as filter feeders (Jeschke *et al.*, 2004), for which combing suspended particulates from the water via filtering structures constitutes foraging.. This is because handling time (time spent processing the prey) must be negligible, the animal must forage at the maximum rate with maximum effort, and the animal must be able to perform foraging and non-foraging activities simultaneously. However, animals can vary in functional response ontogenically and Type I responses have been observed at specific stages of the lifecycles of animals including crabs (Long and Whitefleet-Smith, 2013).

Type II functional responses occur when an animal's capacity to consume their prey is limited by some factor (such as handling), reducing consumption rate as prey density increases,

eventually plateauing when the processing rate of prey reaches saturation. As such, when testing for functional responses, a negative linear coefficient indicates Type II (e.g. Mohaghegh *et al.*, 2001; Zimmermann *et al.*, 2015). Type II functional responses are considered ecologically 'destabilising' (e.g. Barrios-O'Neill *et al.*, 2015) and thus, can be problematic for ecosystem functioning. Type II functional responses are considered destabilising as predators displaying Type II response will feed on prey past the point of prey population replenishment, throwing the prey population out of equilibrium and potentially causing population collapse (Oaten and Murdoch, 1975; Dick *et al.,* 2014).

Higher order predators can cause their mesopredator prey to switch from Type II to stabilizing Type III functional responses, enhancing trophic stability (Post *et al.*, 2000). Type III functional responses are similar to Type II responses, as both responses show a plateau at high prey densities, (i.e. when saturation occurs). However, Type III responses occur when an animal is initially hindered in its ability to consume prey by factors such as learning time (learning the most efficient way to handle the prey) or prey switching, then becomes more efficient at consumption over time. As such, when testing for functional responses, a positive linear coefficient indicates Type III (e.g. Fletcher *et al.*, 2010; Long and Whitefleet-Smith, 2013).

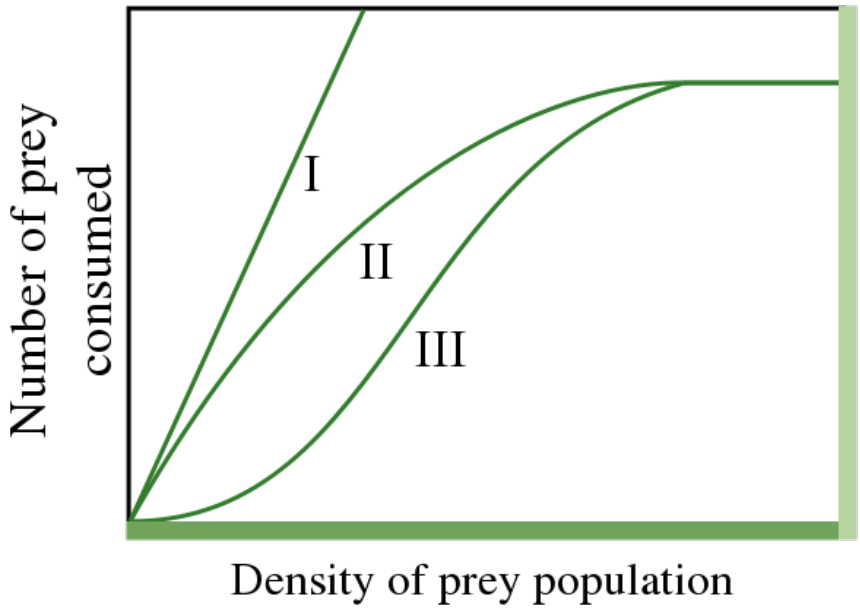

Figure 4.1 The relationship between prey consumption and prey density that are indicative of the 3 major types of functional response. Source: Professor Moorcroft (2009) via Wikimedia Commons.

To determine whether the functional responses of multiple fish could be predicted by multiplying individual responses, Wasserman *et al.* (2016) used predicted, multiplied, consumption of a single fish and compared this to observed responses of multiple fish of both the same and different species. To enhance such assessment methods, measures incorporating predator abundance alongside *per capita* feeding rates have been shown to have strong predictive power (Dick *et al.*, 2017; Dickey *et al.*, 2018) and thus, this method was chosen here.

4.2.4. Aims and objectives

Here I aimed to determine whether the crab species *Carcinus maenas* displays a Type II functional response, as found in destructive invasive species, and to investigate the mediating effects of prey density, conspecific presence, and spatial availability, on prey consumption by

C. maenas. The objective was to record the number of blue mussel (*Mytilus edulis*) spat consumed by these crabs at different levels of prey density and conspecific presence. To determine the impact of spatial availability vs conspecific antagonism, clay discs were applied to specific treatments to mimic the space inhabited by conspecifics as a form of experimental manipulation.

4.2.5. Hypotheses

It was hypothesised that both prey density and conspecific presence would alter crab predation success. It was predicted that crabs would display Type II functional responses, with increasing predation success as prey density increased, plateauing as handling time became restrictive. Furthermore, it was also predicted that an increase in conspecific presence would decrease predation success to a greater extent than disc presence as antagonistic interactions became more likely.

4.3. Methods

4.3.1. Experimental Design

The experiment consisted of five treatments: [1x crab], [2x crab], [3x crab], [1x crab + 1x disc], [1x crab + 2x discs]. 'Discs' refers to baked clay discs of the same approximate size as the crabs that were used as replacements for live crabs in some treatments in order to quantify the effects of conspecific behavioural interactions vs spatial reduction caused by conspecific presence. For each crab/disc treatment, five mussel spat (small, post-juvenile mussels) prey densities were provided (2, 4, 8, 16, 32). Each crab/density combination was replicated three times, for a total of 75 trials. See Figure 4.2 for a summary of this experimental design.

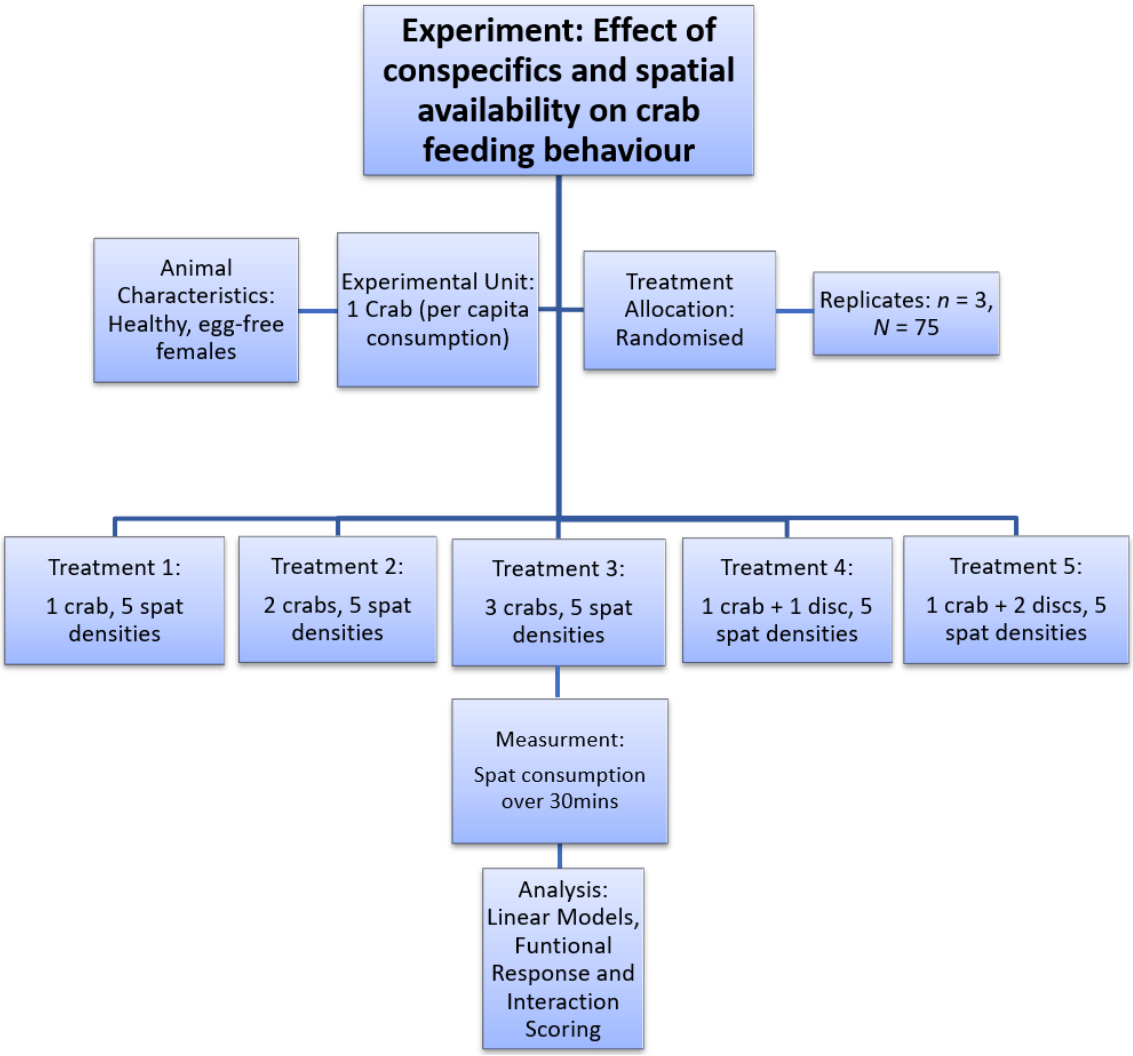

Figure 4.2 Experimental design used to carry out the experiments. Animal characteristics, experimental unit, treatment allocation, treatment groups, measurement and analysis type are displayed.

4.3.2. Animal Husbandry and Size Selection

Female *C. maenas* without eggs, free of visible injury and external parasites (n = 54, mean carapace width 57.63mm ± 0.58mm) were used for this experiment. Crabs were collected in the locality of Strangford Lough, Northern Ireland and were maintained in a large flow-through, sand-filtered, seawater (~13°C) tank enriched with rocks and brown algae. Crabs were fed every two days with a mixture of herring (*Clupea harengus*) and crushed *Mytilus edulis* mussels. *M. edulis* spat were collected at nearby Horse Island, Strangford Lough. Spat

were sorted into size classes by shell length, using 5mm cohorts, in order to determine the most appropriate size class to be used in the experiments. Spat were maintained in flow-through seawater containers, with individuals 10-14.9mm long being selected for the experiments, due to their high abundance in samples and what was deemed to be their relatively energetically enticing size.

4.3.3. Setup

Experimental trials were carried out over one week between August and September 2018, in 30 flow-through, sand-filtered, seawater (~13°C from source) arenas (7L clear plastic boxes, dimensions: 260 x 165 x 140mm). Arenas had lids to reduce disturbance and prevent escape. In specific treatments, baked clay discs were used as a spatial replacement for a live crab in order to distinguish between the effects of the reduction in spatial availability caused by conspecific presence vs the antagonistic interactions caused by conspecific presence. Discs were the same approximate diameter as the mean crab carapace width (~58mm) and were ~20mm thick, placed in the centre of the arenas and added 30 minutes in advance of the introduction of predators. Twenty-four hours before trials commenced all food was removed from the holding tank, to allow for pre-experimental starvation.

Crabs were selected randomly from the holding tank and trials commenced upon the addition of the crabs to the arenas containing prey. Three experimental runs of each treatment combination were (i.e. five predator treatments x five spat densities were performed, terminating after 30 minutes). After the trials, crabs were removed from the arenas and placed into a specific holding tank and fed. Only the crabs used during the experiment were kept in this holding tank, at the exact number required for all trials (75), ensuring that all crabs were deployed the same number of times. All crabs were given 24 hours to recover before

the next pre-experimental starvation period. See Figure 4.3 for illustration of this experimental setup.

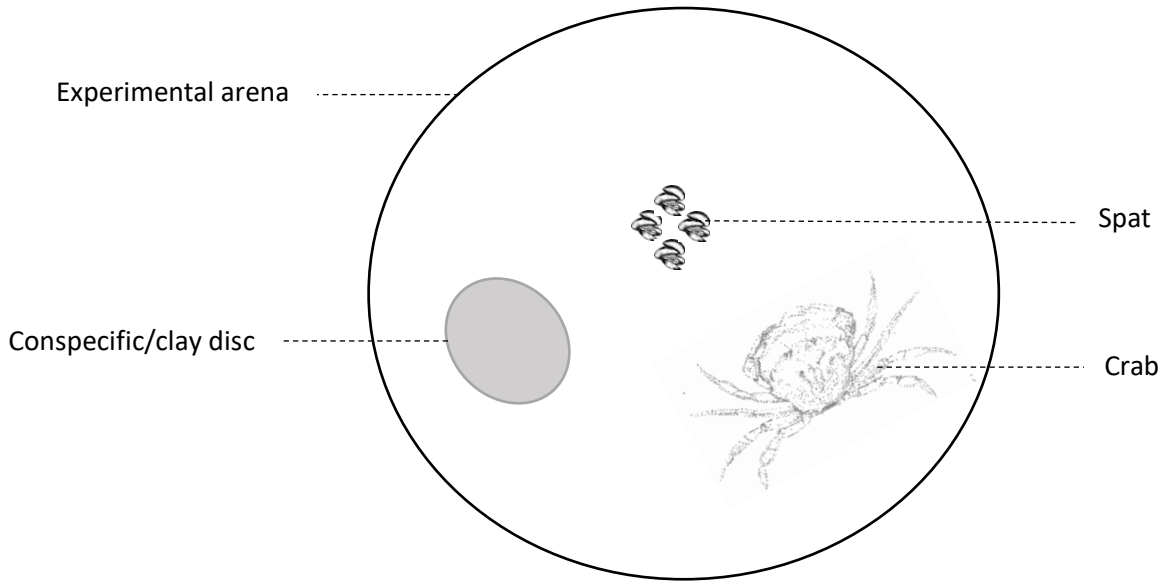

Figure 4.3 Experimental setup, showing placement of spat, crabs and conspecifics/discs within the experimental arenas.

4.3.4. Statistical analysis

4.3.4.1. Functional responses and proportional prey consumption

Data were analysed using R version 4.0.3 (R Core Team, 2020). Proportional prey consumption (i.e. consumption divided by initial prey density) in the functional response experiments was compared using generalised linear models (GLMs) with quasi-binomial distribution, due to residual overdispersal being detected and the data following a roughly binomial distribution Predator treatment and prey density were the computed factors for these GLMs. For each predator treatment, logistic regression of the proportion of prey killed as a function of prey density was used to discern functional response types (*sensu* Juliano, 2001). Where a

significant negative first order linear coefficient was detected, a Type II response was determined; conversely, a Type III form was considered when a significant positive first order linear coefficient was followed by a significant negative second order coefficient (Juliano, 2001). As crabs were not directly observed or recorded via video during interactions, Rogers' random predator equation for non-replacement of prey was applied to estimate values of '*h*' (handling time) i.e., the amount of time spent handling the prey, and '*a*' (attack rate) i.e., the number of attempted attacks over time (Rogers, 1972):

$$N_e = N_0(1 - \exp(a(N_e h - T)))$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, *h* is the handling time, *a* is the attack constant and *T* is the total experimental period. Derived from Rogers (1972), the attack constant in this equation is from experiments in which sandpaper discs were randomly searched for by blindfolded subjects and 'removed', simulating predation, at multiple 'prey' densities. The total number of these discs removed (attacked) increased over time, but at a decreasing rate, due to reduction in prey availability and thus, increased searching/handling time. This allowed for the calculation of an attack coefficient, which forms the basis of the attack constant in the current equation. Model fitting used the Lambert W function (Bolker 2008) in R due to the implicit nature of the random predator equation (i.e. the random predator equation is not solvable on its own).

The FR parameters derived from observed single-predator experimental treatments were then used to predict and fit multiple predator FR curves using a population-dynamic model following McCoy et al. (2012) and Sentis and Boukal (2018):

$$\frac{dN}{dt} = -\sum_{i=1}^{n} f_i(N)P_i$$

where N is the prey density, P_i (i = 1, 2, …, n) are the population densities of predators i and $f_i(N)$ is the FR of predator i. The population-dynamic method has been deemed the most robust way of assessing MPEs in functional response studies, and one that accounts for prey depletion and non-linear feeding rates (Sentis and Boukal, 2018).

4.3.4.2. Non-trophic interaction scores (ISNTs)

Predicted multiple predator outcomes were calculated by multiplying the results from the single predator treatments to simulate an increase in predators (e.g. 2*[1x crab], 2*[1x crab + 1x disc], 3*[1x crab], 3*[1x crab + 2x disc]). These were then compared to observed multiple predator functional responses (i.e. appropriate [2x crabs] and [3x crabs] treatments) using Interaction Scores (IS). For both observed and predicted responses, Interaction Scores (IS) were calculated as:

$$IS = \frac{Prey\ Eaten}{Prey\ Density}$$

Predicted IS were then subtracted from observed IS to achieve Non-Trophic Interaction Scores (ISNTs) for multiple predator treatments. The more negative an ISNT, the more antagonistic the interaction was, as this represented a decrease in *per capita* crab feeding, while the more positive an ISNT, the more synergistic the interaction was, representing an increase in *per capita* crab feeding. ISNTs were then compared across prey densities and predator treatments using GLMs, assuming a quasi-binomial distribution due to overdispersal. Comparisons of

predicted and observed multiple predator experimental treatments allowed for the quantification of non-trophic interactions, such as Multiple Predator Effects (MPEs). This approach allowed comparisons to be made between predicted and observed multiple predator outcomes.

4.4. Results

4.4.1. Functional responses and proportional spat consumption

Prey survival in controls was 100%, allowing us to attribute all experimental mortality to predation, further confirmed by crushed shell remains in the arenas. Type II functional response curves were found for all predicted/observed treatment combinations (Figures 4.4, 4.5). Proportional spat consumption was significantly decreased by both crab treatment ($F_{4,69}$ = 3.32, $p < 0.05$) and prey density ($F_{1,73}$ = 81.15, $p < 0.05$), see Figure 4.6.

4.4.2. Non-Trophic Interaction Scores (ISNTs)

Prey density significantly increased ISNT scores for treatment groups [2x crab] and [1x crab + 1 disc] ($T_{1,29}$ = 3.07, $p < 0.05$), increasing feeding synergy. There was no significant effect ($p > 0.05$) of crab treatment between [2x crab] and [1x crab + 1 disc] (Figure 4.7). Conversely, crab treatment had a significant effect on ISNT scores between treatment groups [3x crab] and [1x crab + 2discs] ($T_{1,29}$ = -3.35, $p < 0.05$), with ISNT scores being consistently lower (more antagonistic) in treatment group [3x crab]. There was no significant effect of prey density between treatment groups [3x crab] and [1x crab + 2 discs] (Figure 4.8).

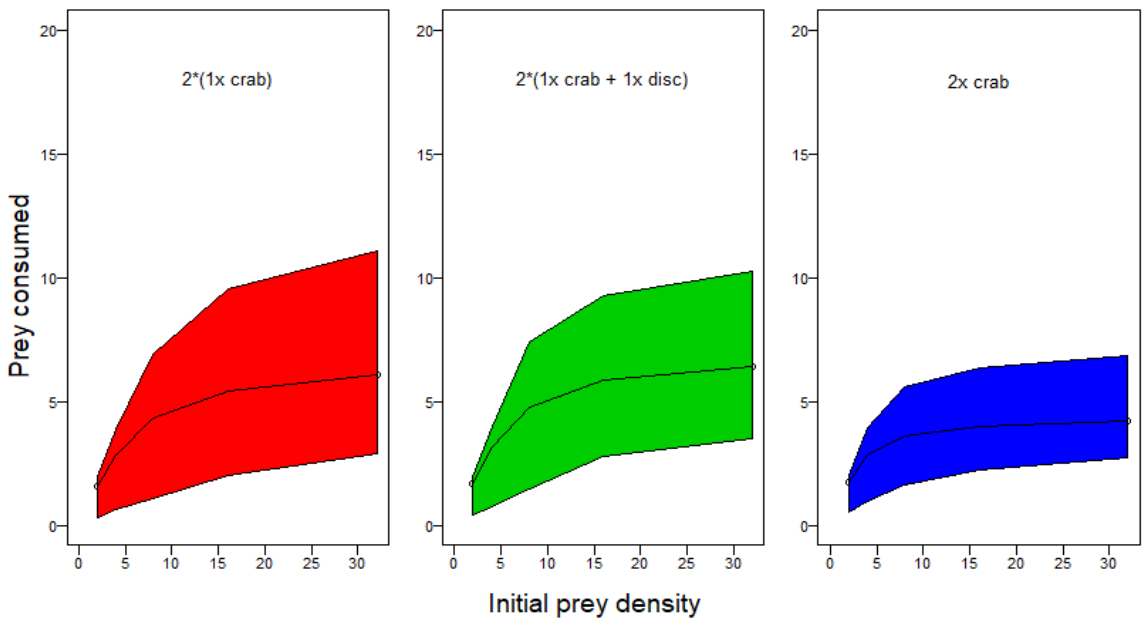

Figure 4.4 'Type II' functional responses for treatment groups 2*(1x crab), 2*(1x crab +1x disc) and 2x crab. Initial prey density (No. of *M. edulis*) along x-axis, prey consumption by crabs within 30mins on y-axis.

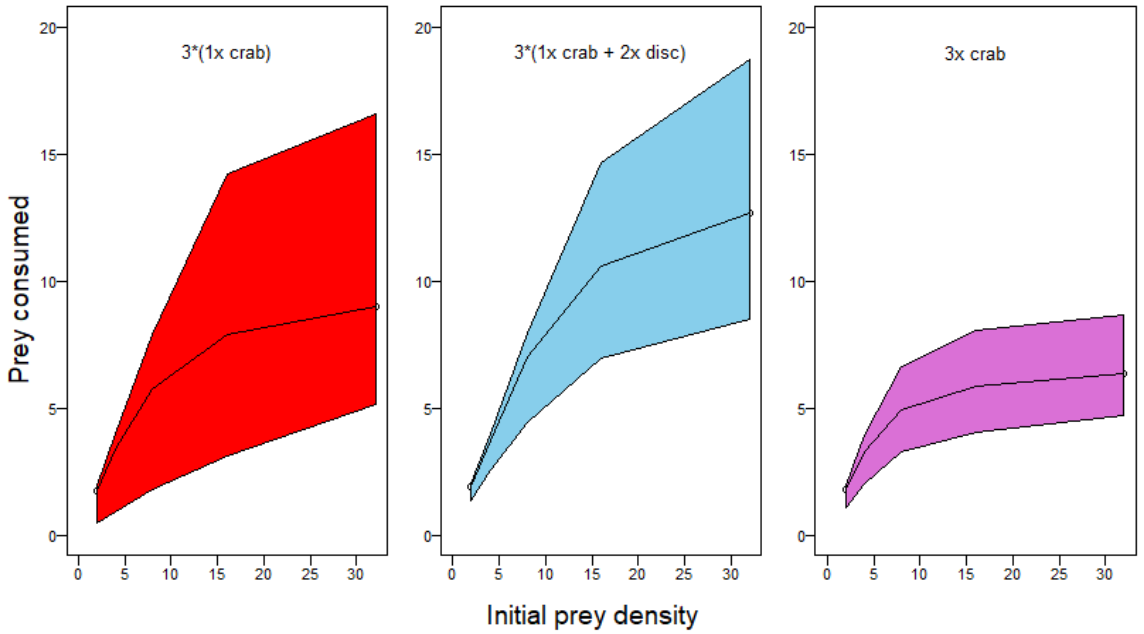

Figure 4.5 'Type II' functional responses for treatment groups 3*(1x crab), 3*(1x crab +1x disc) and 3x crab. Initial prey density (No. of *M. edulis*) along x-axis, prey consumption by crabs within 30mins on y-axis.

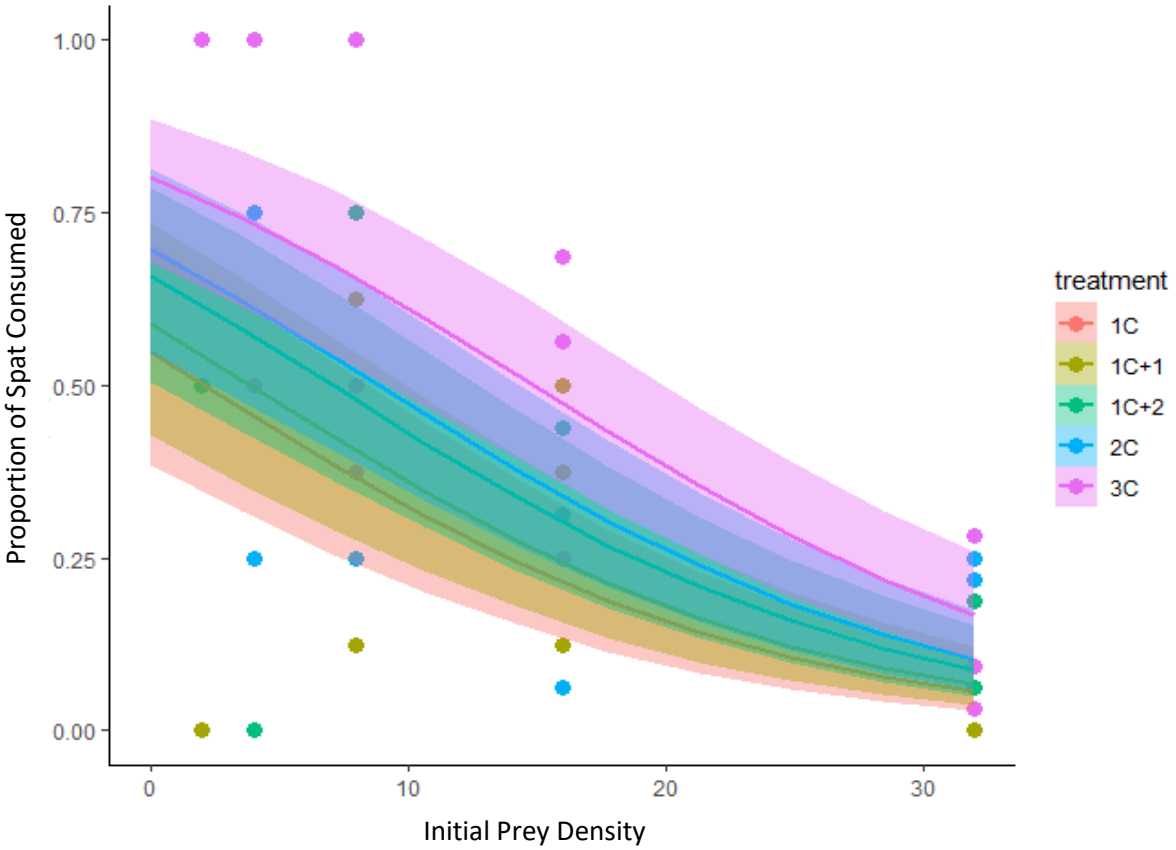

Figure 4.6 Proportional consumption of *M. edulis* spat across all treatment groups. Proportion of consumed spat displayed on y-axis, initial mussel prey density displayed on x-axis, crab predator treatment group depicted in colour fill (legend).

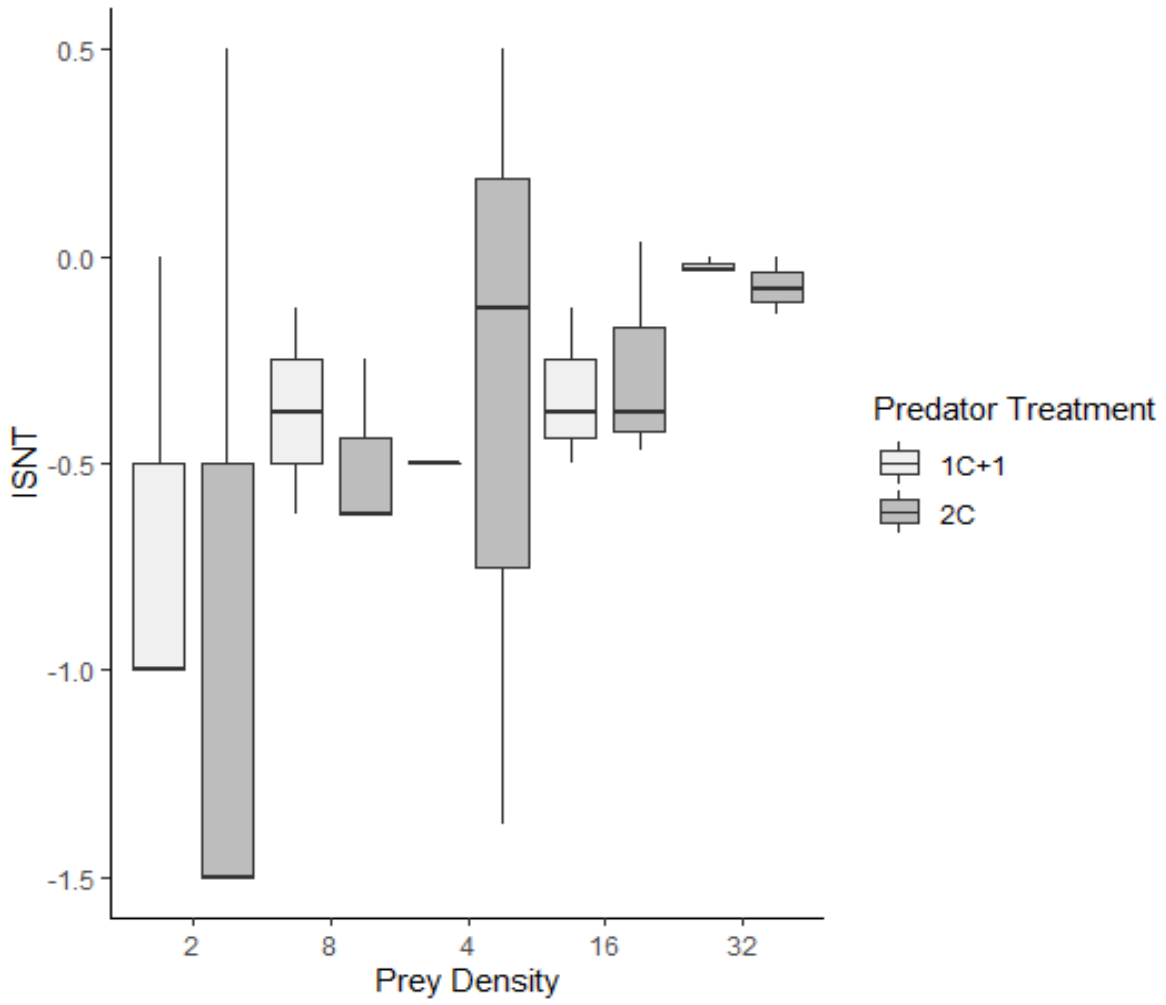

Figure 4.7 ISNT scores across treatment groups 1C+1 (1x crab + 1x disc) and 2C (2x crab). ISNT score displayed on y-axis, initial prey density displayed on x-axis, predator treatment depicted in fill (legend).

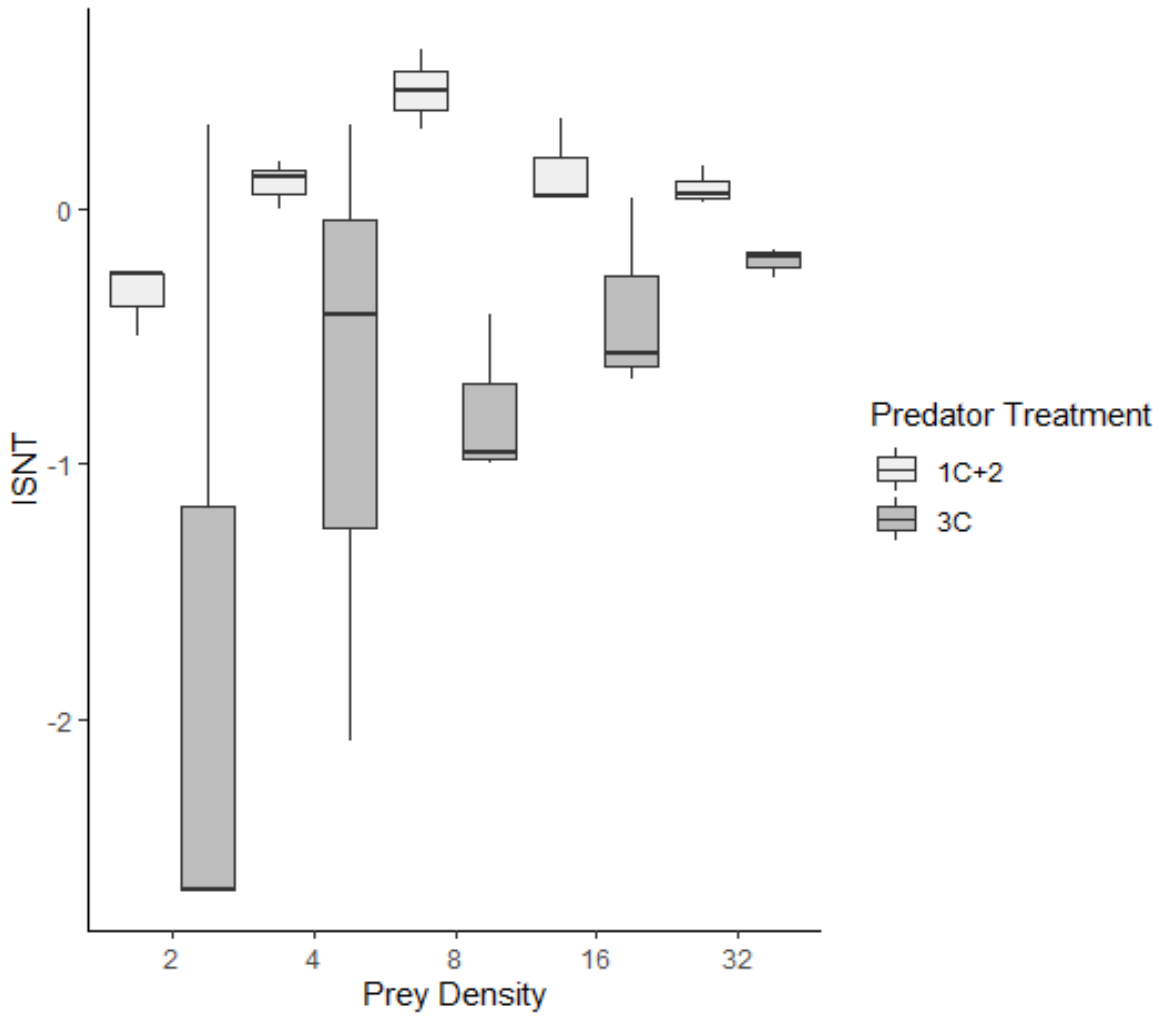

Figure 4.8 ISNT scores across treatment groups 1C+2 (1x crab + 2x disc) and 3C (3x crab). ISNT score displayed on y-axis, initial prey density displayed on x-axis, predator treatment depicted in fill (legend).

4.5. Discussion

4.5.1. Proportional prey consumption and functional responses

Across all treatments, *C. maenas* crabs displayed destabilising Type II functional responses, but displayed varying degrees of antagonistic interactions based on conspecific presence, which impacted feeding synergy. These results demonstrated that fear-released mesopredators can display destabilising Type II functional responses (Barrios-O'Neill *et al.*, 2015), comparable to that of invasive species. While further studies directly comparing mesopredator functional responses in the presence and absence of higher predators are needed, Chapters 2 and 3 of my thesis support these findings given that mesopredator suppression occurred across multiple species from a marine mesopredator guild.

Furthermore, the results here showed that as prey density increased, overall proportional prey consumption decreased, and at higher prey densities, no crabs consumed all of the available prey. This result is consistent with previous findings that crabs cannot efficiently handle high densities of bivalve prey (Wong and Barbeau, 2006). *M. edulis* reproduces prodigiously, generally in late Spring through Summer (Seed, 1969; Wilson and Seed, 1974), with recruitment occurring year round (Kautsky, 1982), maintaining carrying capacity. The results of the current study suggested that such a reproductive strategy could be effective at buffering *M. edulis* recruitment against predation by mesopredators such as *C. maenas*. *M. edulis* reproductive strategy could bombard *C. maenas* crabs with high densities of spat. This strategy is similar to that observed in instances of eelgrass seed predation by *C. maenas*, whereby crabs are overwhelmed by high numbers of seeds over large spatial scales (Infantes *et al.,* 2016). This could enhance mussel recruitment and reduce susceptibility to overgrazing by mesopredators, benefitting ecosystem health, as biogenic mussel reefs are associated with

high biodiversity and enhanced habitat complexity (Commito and Rusignuolo, 2000; Kristensen *et al.,* 2015; Norling and Kautsky, 2007; Saier, 2002; zu Ermgassen *et al.*, 2020). Moreover, the functional response results here highlighted the complex role that spatial availability plays in predator-prey interactions, as found in previous studies (Fraker and Luttbeg, 2012; Sih, 2005) and how this is linked individual behaviour and conspecific tolerance. Specifically, while there was no noticeable difference in functional response between crab and disc treatments at the two-crab level, crabs had greater predation success (and thus higher peaking FRs) in the presence of discs at the three-crab level. This shows that with decreasing spatial availability, *C. maenas* predation success increased. Despite the potential for prey refugia and handling time to increase as clay disc presence increased, individual *C. maenas* benefitted from the decrease in spatial availability. This finding suggestedthat *C. maenas* foraging is optimised in instances of low conspecific density combined with low habitat complexity and spatial availability. While the results presented here are promising, further study is required to elucidate the strength of these effects in a more open experimental environment, as the experiments were limited to relatively small plastic arenas.

4.5.2. Non-trophic interaction scores (ISNTs) and antagonistic interactions

Our ISNT score results showed that at a lower conspecific abundance, feeding synergy between conspecifics was primarily driven by prey density, with an increase in prey density making interactions less antagonistic. At a higher conspecific abundance, prey density had no effect, with feeding synergy being primarily driven by conspecific abundance. This is evidence that *C. maenas* resource sharing and co-existence is mediated by prey density when conspecific abundance is low, switching to a combination of trait mediation (antagonism) and

density mediation (conspecific density) as conspecific abundance increases. This interplay between prey density and conspecific presence supports previous findings that both prey density and predator traits must be considered when assessing predator-prey interactions, as both can influence the rate and outcome of predator-prey interactions (Liu *et al.*, 2018). For example, aphids display wing polymorphism based on predator presence, predator density and attack rate (Kunert and Weisser, 2003) and the co-existence of multiple aphid species is mediated by predator density and attacks, as well as reduced foraging efficiency due to competition (van Veen *et al.*, 2005).

Furthermore, Liu *et al* (2018) emphasised that while raw predation rate can increase as density and conspecific abundance increase, the likelihood of antagonistic behaviour and thus, resulting injuries, increased. This would suggest a decrease in fitness with increasing antagonistic behaviour among conspecifics. However, there is evidence that antagonistic interactions towards conspecifics can facilitate the spread of a species, with aggressive individuals either inhabiting the range frontier, or displacing conspecifics for access to optimal established habitats (Groen *et al.*, 2012). Previous studies also showed that evidence that mesopredator release can facilitate range expansion in fish (Lapoint *et al.*, 2015), thus, bolder more antagonistic individuals within a fear-released population my benefit from the loss of fear of predation to a greater extent, compounding the negative effects of fear-release.

Conversely, a lack of aggression towards conspecifics has been shown to facilitate coexistence at high densities in invaded ranges (Suarez *et al.*, 1999). For *C. maenas* in particular, the negative impacts caused by antagonistic interactions with conspecifics can lead to lower ecological success, as seen in Griffen and Delaney (2007). These authors investigated the replacement of the invasive *C. maenas* by a more recent invader, the Asian shore crab, *Hemigrapsus sanguineus*. They found that *C. maenas* displayed substantially higher rates of

conspecific aggression compared to *H. sanguinieus*, and as a result, *C. maenas* was being replaced as the dominant species in the intertidal zone. So, while antagonistic interactions may initially enhance *C. maenas*' ability to extend its range and invade new areas, its intolerance of conspecifics can hinder its success. These findings highlight the importance of accounting for conspecific antagonism in predator-prey research.

4.5.3. Ecological consequences

The combined metrics from the current study showed that female *C. maenas* were at optimal bivalve foraging success in conditions of low prey density and low conspecific competition. These results support previous findings on *C. maenas*' aggressive behavioural tendencies, as they tend to be more aggressive in clumped, high density prey areas (Tanner *et al.*, 2011). The current study linked this behavioural response to destabilising effects using functional response techniques, which, a thorough examination of the scientific literature indicated, had not been done before. Our results also demonstrate that methods commonly used in invasive species research are effective at quantifying the impacts of fear-released species. As such, fear-release species should be considered in a similar way to invasive species, in that their feeding rates and feeding behaviours are analogous and can be successfully analysed using the same techniques.

However, crabs are not uniform in their tolerance of conspecifics, with some species maintaining high population densities with low aggression, such as *H. sanguinieus* (Griffen and Delaney, 2007), while others maintain both high populations densities and higher aggression (Pintor *et al.*, 2009). It is important to account for these behavioural discrepancies (Lohrer and Whitlatch, 2002) in order to address species shifts within ecological communities. Chapter 3 of my thesis addressed the effects of these inter-species discrepancies, by

investigating mesopredator suppression across multiple crabs from a marine mesopredator guild (including *C. maenas*). The findings of that chapter supported the findings of this chapter, as all the crabs investigated were found to have negative cascading effects on their prey in the absence of a higher predator, with slight differences in feeding rate. These findings suggested that while this crab mesopredator guild display small differences in foraging success, they all have the potential to destabilise and degrade ecosystems in instances of fear-release.

Chapter 5

Friend or foe: Variation in fear response in the crab *Carcinus maenas* via infrared cardiac sensing

Impact Statement

There was a follow-up study planned for this chapter which would have involved the direct recording of changes in electromagnetic activity associated with crab responses to predator cues and the potential for crabs to use electromagnetic camouflage. However, this research became untenable during the pilot stage due to COVID-19 restrictions and technical difficulties. As such, planned work to expand on this chapter's findings did not take place.

5.1. Abstract

Fear responses in prey species have been well studied using behavioural assays. However, the underlying physiological responses that drive these behaviours are less well studied and can provide greater insight into the biological stress being experienced by prey animals. In this study the cardiac responses of an ecologically important brachyuran crab, *Carcinus maenas* were recorded in response to two chemical cue treatments and a control: a known predator, the elasmobranch *Scyliorhinus canicula*; a known non-predator, the herbivorous/detritivorous fish *Chelon labrosus*; and a blank seawater control. A total of 26 replicates were performed. Crab cardiac activity changed more frequently, more intensely and for longer in response to the predator (*S. canicula*) cue and the blank seawater control vs the non-predator (*C. labrosus*) cue (all $p<0.05$). This is evidence of not only the differentiation between known predators and non-predators, but also between clear and cryptic threats. These findings demonstrated a nuanced physiological response to predator cues based on predator identity, which can enhance energy use during fear response in brachyuran crabs. Given the frequency of behavioural freezing or 'tonic immobility' in decapod crustaceans, this study highlighted the importance of recording physiological data when investigating predator-prey interactions.

5.2. Introduction

5.2.1. Cardiac Activity and the Cost of Predator-Induced Stress

Animal stress physiology and individual fitness are integrally linked (e.g. Möstl and Palme, 2002; Boonstra, 2013; Beausoleil *et al.*, 2018). In the marine environment, for example, crabs choose less profitable prey in order to preserve claw integrity (Smallegange and Van Der Meer, 2003), showing a clear link between physiological feedback and behavioural choices leading to enhanced health and fitness. A key contributor to animal stress in nature is predation risk which can affect prey demography, ecological community structure, and ecosystem processes (Sheriff and Thaler, 2014). Therefore, measuring the physiological effects of predation risk, such as predator induced stress, can provide important insights into the biological costs of the fear of predation.

Stress in animals can have significant effects on cardiac activity (Li *et al.*, 2000; von Borell *et al.,* 2007 Hourdez, 2018), making cardiac assays a robust method for determining the impact of predation stress on animals (e.g. Höjesjö *et al.*, 1999; Rovero *et al.*, 1999; Johnsson *et al.,* 2001). In the context of predator induced stress, changes in cardiac rhythm and beat rate have been linked to anti-predator responses via the fight or flight mechanism (Robinson, 2018). The fight or flight cardiac response has been observed across a diverse range of taxa from arthropods (Adamo *et al.*, 1995), to mammals (Ford and Reeves, 2008). These cardiac responses have associated energetic costs, as measures such as heart rate are intrinsically linked to metabolic rate (Green, 2011).

5.2.2. Non-Consumptive Effects of Predator-Induced Stress in Aquatic Systems

Predator-prey interactions are not exclusively consumptive and can lead to death of an organism without any physical contact (Preisser *et al.,* 2005). Pressier *et al.* (2005) discussed the fact that the studies in aquatic systems found more prominent indirect effects of fear and intimidation than studies in terrestrial systems. As described in Cox and Lima (2006), terrestrial systems have historically undergone more homogenising biotic effects than aquatic systems, which remain more heterogenous in their predation regimes. This distribution of aquatic predator regimes in is reflected in the increased strength of top-down effects and subsequent trophic cascades observed in marine and freshwater systems (Shurin *et al.,* 2002). As aquatic systems can display a greater diversity of predator effects than terrestrial systems, developing methods for recording the physiology of predator induced stress responses can enhance the scientific understanding of impacts on species fitness and ecology in aquatic ecosystems.

5.2.3. Photoplethysmography, Stress Mitigation and Methodology Chosen

The intensity of predator-induced stress responses can vary based on context; for example scallops that are near refuges have a lower cardiac response to the presence of predators than more exposed scallops (Kamenos *et al.,* 2006). This context-based variation is important when recording predator-induced stress, as animals can behaviourally respond to a predator in a manner that masks underlying physiological changes. For example, recording behavioural freezing such as tonic immobility (Erhard *et al.*, 1999) by behavioural assay alone, would suggest a halting of activity. However, cardiac recording can show significant ongoing physiological changes even when observable behaviour has ceased.

There are multiple methods for recording changes in cardiac activity in marine fauna. For example, measuring corticosteroid levels, a frequent method in mammalian and teleost studies (Clearwater and Pankhurst, 1997; Loseto *et al.*, 2017; Keogh *et al.,* 2020) or surgically implanting data loggers, a more recent development (Laske *et al.*, 2021) that has been applied to decapod crustaceans (McGaw *et al.,* 2018). A common method of recording cardiac activity in decapod crustaceans involves surgically placing wires and electrodes into the cardiac tissue (Bierbower and Cooper, 2009; Burnovicz *et al.*, 2009; Forgan *et al.*, 2014; Hourdez, 2018). This is a concern for experimental design, given the evidence of the ability to feel pain in decapod crustaceans (Elwood *et al.*, 2009; Elwood, 2012).

Elwood (2009) demonstrated that crabs do not simply react to harmful stimuli via nociception, but that they 'remember' painful stimuli and avoid known sources of harm. Furthermore, animals react heterogeneously to stress and trauma (Cohen *et al.,* 2003), meaning animals undergoing invasive surgery etc. have the potential to react independently. Thus, when attempting to detect acute changes in cardiac activity in association with a specific cue, it is important to minimise undue stress to the animal under investigation, as stress and trauma can substantially alter cardiac activity (Huang *et al.*, 2013; von Borell *et al.*, 2007; Wilson *et al.*, 2017).

However, recent developments in sensor technology have allowed for the successful use of non-invasive cardiac studies on marine invertebrates via infrared photo-sensing (e.g. Pautsina *et al.* 2014; Bakhmet *et al.* 2015). The technique of using infrared phototransistors to record cardiac data on decapod crustaceans was pioneered in the 80s (Depledge, 1984) and has undergone multiple refinements since (Depledge 1984; Aagaard *et al.* 1991; Pautsina *et al.* 2014; Bakhmet *et al.* 2015). This is known as photoplethysmography, and was initially

developed to record cardiac finger pulses for human health use in the 1930s (Hertzman and Spealman, 1937; Alian and Shelley, 2014).Photoplethysmography has proved an effective, non-invasive method for recording the cardiac activity of marine invertebrates. As such, it was deemed an appropriate method of recording predator-induced stress response for the current study.

5.2.4. Brachyuran Cardiac Structure and Brachyuran Species Chosen

Brachyuran crabs are suitable models to test marine invertebrate cardiac responses due to a relatively complex heart that is analogous to the vertebrate heart (Shuranova *et al.*, 2006). Brachyuran cardiac structure is somewhat similar to that found in vertebrates, being partially closed and comprised of a complex network of blood vessels (see Figure 5.1). This allows for the recording of distinct heart beats, making the detection of changes in rhythm and beat rate simple. Brachyurans also exhibit fight or flight responses to predatory cues that are comparable to vertebrates (Canero and Hermitte, 2014). This response can then be observed and measured via changes in cardiac activity (Shuranova *et al.*, 2006).

While there are analogous structures in vertebrate and brachyuran cardiac biology, brachyuran cardiac structure differs from vertebrates in important ways. For example, brachyuran crabs have a partially closed circulatory system (McGaw, 2002, 2005). This is a by-product of the evolutionary process of carcinisation (becoming more crab-like) whereby the nervous and cardiac tissues have become centralised (Davie *et al.*, 2015). In non-carcinised decapods, such as crayfish and lobsters, the cardiac tissue extends down the abdomen (Burnovicz *et al.,* 2009; Hourdez, 2018). This centralised positioning of the brachyuran heart within the body (see Figure 5.2) allows for the easy attachment of sensors.

Furthermore, brachyuran cardiac activity displays additional components to the fight or flight response. The initial cardiac response in brachyurans is arrhythmia (irregular heart beat) followed by bradycardia, a slowing of the heart rate (Canero and Hermitte 2014). This cardiac response has been described as the 'alternate response' and is associated with behavioural freezing (King and Adamo, 2006). In the wild, behavioural freezing in brachyuran crabs is used as an anti-predator response in the form of tonic immobility (O'Brien and Dunlap, 1975). This is a direct link between the physiological and behavioural response of a species to predator induced fear.

To investigate the effects of fear of predation on brachyuran cardiac activity, the common shore crab (*Carcinus maenas*) was chosen for the current study. *C. maenas* has been used successfully in previous cardiac studies investigating other stressors, such as temperature change (Camus et al., 2004; Tepolt and Somero, 2014), tidal change (Styrishave *et al.*, 2003) and chemical irritants/contaminants (Bamber and Depledge, 1997). Additionally, *C. maenas* is locally abundant, being a ubiquitous species on UK and Irish shorelines, and has a wide global distribution, including multiple invasive ranges (Neal and Pizzolla, 2008). This reduced the logistics required for specimen collection, and made the results of our research relevant to the management of invasive species via the suppression of problematic mesopredators in instances of 'mesopredator release', an issue of global concern (Prugh *et al.*, 2009). This made *C. maenas* a suitable organism for the current study.

5.2.5. Chemical Cues and Elasmobranch and Control Species Chosen

Here, olfactory chemical cues extracted from an elasmobranch predator were used to investigate the predator-induced cardiac stress response of *C. maenas*. In the marine environment animals use olfactory information to assess predation risk , for example, fish

(Wisenden, 2015) and bivalves (Castorani and Hovel, 2016). These chemical cues play an important role in ecosystem funtioning, affecting community structure and energy transfer (Hay, 2009) by altering animal behaviour. Decapod crustaceans are known to use predator chemical cues in order to assess predation risk and inform their anti-predator and predator avoidance behaviours (Lavalli and Spanier, 2016). This widespread use of chemical cues by the crustacea has made them effective models for investigating the effects of marine chemical cues (Hay, 2011). The prominence of chemical cues in the marine environment, combined with known efficacy of predator chemical cue on decapod crustaceans made the use of predator chemical cues an appropriate choice for attempting to elicit predator induced stress responses in *C. maenas*.

Initially, the elasmobranch *Mustelus asterias*, the diet of which can consist of over 95% crustacea (McCully Phillips et al., 2020), was considered for the provision of predator chemical cues for this study, but acquisition of specimens proved logisitically untenable at the time. As a result, the more locally available species *Scyliorhinus canicula* was chosen as a replacement. While *S. canicula* is a more generalist feeder (Kousteni et al., 2017), dietary analysis has found that stomach contents can cansist of almost 50% crustacea, including brachyuran species such as *Necora puber* (Henderson and Dunne, 1999). As such, it was likely that *C. maenas* would respond to *S. canicula* as a potential predator and pilot studies confirmed this, so *S. canicula* was an appropriate choice for the provision of chemical cues.

The thicklip grey mullet (*Chelon labrosus)* is a herbivore and detrivore (Freyhof and Kottelat, 2008) and as such, not a crab predator. The species was locally available from Exploris Aquarium, Portaferry N.I., as were *S. canicula* specimens, reducing logistic requirements. Due to these factors, *C. labrosus* was selected as an appropriate species to extract non-predatory

odour from to act as a comparison to the known predator *S. canicula*. A cue of filtered seawater was also used to act as a control. This allowed for the distinction to be made between an initial startle response to a cue and a more prolonged predator-induced stress response.

5.2.6. Aims and Objectives

This study aimed to measure predator-induced stress response in the crab *Carcinus maenas* via cardiac assay. The objective was to record fluxes in heart rate and beat volume, occurrences of cardiac arrest, arrhythmia, and other cardiac nuances in response to chemical cues. To do this, two distinct cues were employed along with a control cue: a blank control of filtered sea water; a chemical cue from *Scyliorhinus canicula*; and a non-predator cue from *Chelon labrosus*. This allowed for the determination of a fear response, separate from that of the response to a novel or unknown stimulus.

5.2.7. Hypotheses

It was hypothesised that fluxes in crab heart rate and beat volume would differ in response to a predator vs a non-predator chemical cue. It was predicted that the crabs increase cardiac activity in response to the predator cue, but that the strength of the response would depend on the treatment.

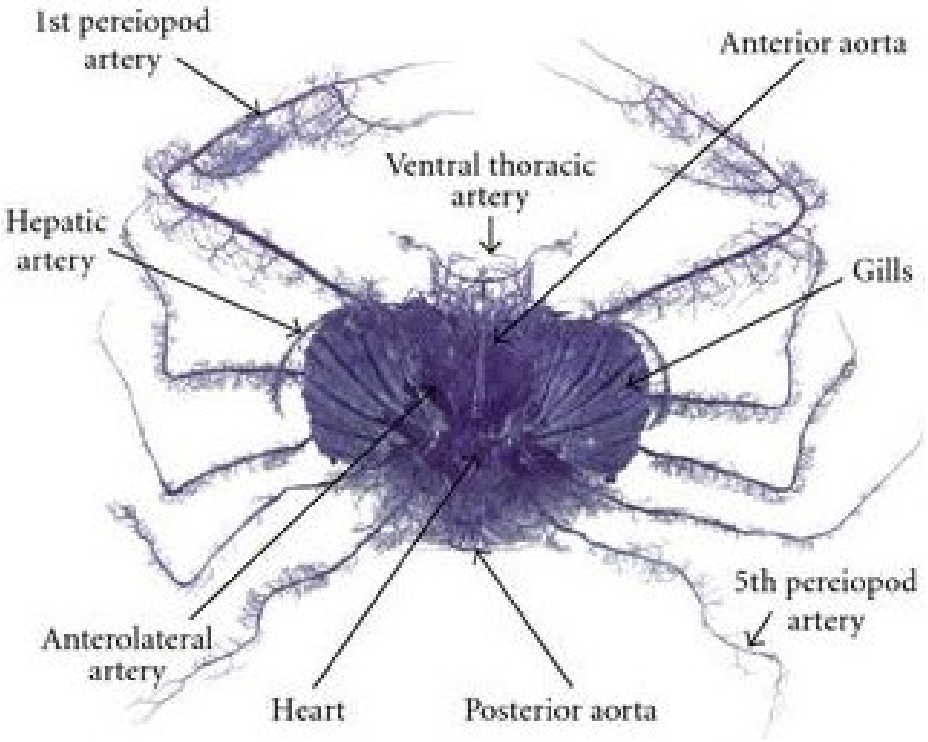

Figure 5.1 Corrosion cast displaying the cardiovascular system typical of decapods. The main arteries are labelled, and the overlying capillary network is visible. Corrosion casts are formed by filling the blood vessels with solidifying resin, then macerating the soft tissue away. Originally from Reiber and McGaw (2009), acquired via Creative Commons (https://creativecommons.org/licenses/by/3.0/).

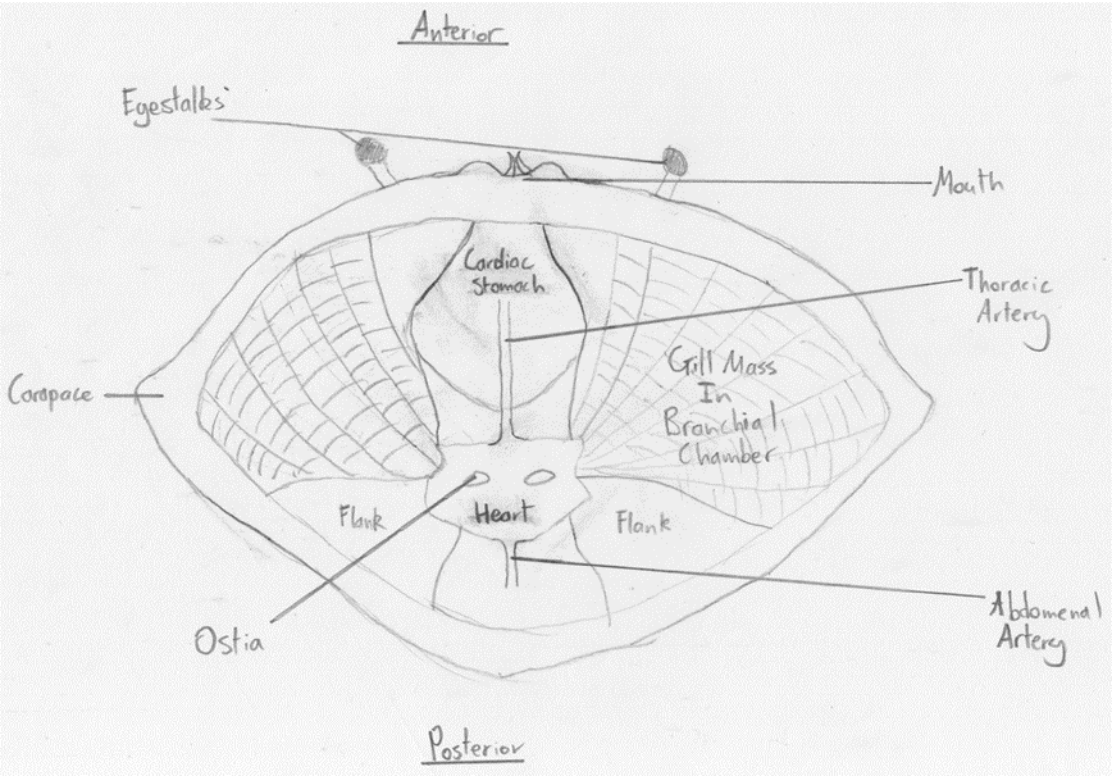

Figure 5.2 Sketch depicting the internal anatomy typical of brachyruans, focusing on cardiac and respiratory tissue. This hand-drawn sketch displays the location of important cardiac structures in relation to other significant structures, such as the cardiac stomach and gills within the brachyuran body plan. This sketch was drawn by the author of this thesis.

5.3. Methods

5.3.1. Experimental design

The experiment consisted of three treatments cues: a known crab predator, *S. canicula* (Henderson and Dunne, 1999); a known non-predator of crabs, *C. labrosus,* a herbivore and detritivore (Freyhof and Kottelat, 2008); and a blank cue of filtered seawater. *S. canicula (N* = 2, body length ~60cm) and *C. labrosus* (*N* = 2, body length ~30cm) were obtained from Exploris Aquarium, Portaferry, N.I. Intact male shore crabs, *C. maenas* (*N* = 78, carapace width 55-65mm), were collected in the vicinity of Ballyhenry Island, Strangford Lough, N.I., used once and then released. A total 26 replicates were carried out and treatment allocation was randomised. Both heart rate (beats per minute) and beat volume (voltage output from infrared sensors) were recorded.

5.3.2 Experimental setup

The cardiac activity was recorded using custom built infrared (IR) sensor cables attached to an ADInstruments PowerLab 26T data recorder, running the software LabChart, version 8.0.5. The ADInstruments PowerLab 26T is a data acquisition device that is compatible with multiple input devices, including electronic infrared sensors, as used here. See figure 5.3 for a diagram of the experimental setup. The sensor cables consisted of an IR photoelectric optical sensor (model type RPR220), metal film resistors, six core insulated alarm wire, and DIN pin connectors. The flexible insulated wire allowed for the relatively free movement of the crabs. The sensors were waterproofed using heat shrink plastic and sealed using epoxy around the seams. See figure 5.5 for images of the wire components.

Initially, cyanoacrylate gel and dental wax were trialled to adhere the sensors to the crabs' carapaces. Cyanoacrylate gel was found to be too rigid and crumbled easily and dental wax provided poor adhesion to the carapace surface. Fast-curing epoxy was found to be an effective adhesive for attaching the bungs to the crab carapace. Attaching the sensor directly to the carapace caused excessive rigidity at the connection point, often causing the sensor to detach from the carapace. To solve this issue, rubber bungs with a hole drilled through the middle were attached to the dorsal surface of the crabs' carapace using 'Bond Together' epoxy resin (Figure 5.6). The bungs held the sensor cables in place, while providing sufficient flexibility to compensate for small movements from the crab. The sensors were further waterproofed using transparent laboratory film placed over the sensor head before insertion into the rubber bungs.

The rubber bung attachment process took ~20 minutes per crab and was carried out in batches of six crabs simultaneously. During this process the crabs were kept moist on paper towels and were then immediately placed in glass holding tanks after the bung attachment, to acclimatise overnight (~22hrs). Full curing of the epoxy occurred before the crabs were placed into their holding tanks, to mitigate the effects of epoxy leaching, which would be detrimental to the crabs and effect the results. The holding tanks were supplied with a flow-through of filtered seawater. The rubber bungs were carefully removed immediately after experiments to prevent carapace damage and the crabs were released the next day.

Prior to the bung attachment process, crabs were maintained in two identical 80cm x 60cm x 40cm opaque grey plastic flow-through tanks and fed *ad libitum* on Atlantic herring. Crabs were kept in stock no longer than one week before bungs were attached, ready for experimental use.Data was recorded for six minutes per crab, with a 10-minute rest period

beforehand to reduce the effects of handling. Immediately prior to the 10-minute rest period, crabs were taken from the holding tanks and the infrared sensors were placed into the bungs on their backs and they were then placed into the experimental containers, a process taking less than one minute. This process was carried out quickly and carefully to minimise handling time and reduce stress.

The 'baseline phase' of recording was always the first minute after the 10-minute rest period. The 'shock phase' of the recording was always one minute into the 6-minute recording period, when the cue was added. The 'final phase' of recording was always the last minute of the 6-minute period. Six minutes of recording per crab was chosen to allow for a consistent amount of time after the reaction of the crabs to the cues, as these reactions never lasted longer than one minute. This timing meant that the crabs were always in the experimental containers for ~16 minutes total. See Figure 5.4 for a summary of the experimental design.

The containers used to hold the crabs for the duration of the data recording were made of opaque grey plastic and were 27cm x 16.5cm x 11.5cm, containing 2ltrs of filtered seawater. The containers were covered with black flexible plastic lids to reduce the effects of observer presence. These experimental containers were placed on metal racks in water baths that were 56cm x 32cm x 20cm and kept at 13°C to maintain a constant temperature.

5.3.3. Cue collection

S. canicula were maintained in a 220cm x 130cm x 100cm fibreglass flow-through tank and fed *ad libitum* on Atlantic herring (*Clupea harengus*). *C. labrosus* were maintained in an identical setup and were fed using aquarium standard feed pellets.

Prior to experiments, one individual of both *S. canicula* and *C. labrosus* were moved to two smaller flow-through seawater tanks (120cm x 60cm x 60cm), that lacked enrichment, 16 hours before experiments began to reduce the effect of environmental odours. Chemical cues were extracted from the individual specimens using sterilised cotton swabs rubbed along the side of the body, the underside of the body and near the gills. This method is similar to that used for mucus collection on larger shark species (*sensu* Lieber *et al.* 2013), but using a less abrasive medium and on a much smaller scale as the *S. canicula* specimens used were less than 1m long. The swabs were then immediately placed into 100mls of filtered seawater and mixed thoroughly. A 50ml sample of this infusion was extracted via syringe and was used as the chemical cue for the experiment. Cue collection was carried out immediately prior to use in an experiment, within minutes of being used, to improve retention of the cue (i.e. freshness). All three experimental species were fed *ad libitum*, but to ensure consistency and mitigate the effects of contamination of chemical cue samples by food odours, they were not fed for 24 hours prior to experimentation.

5.3.4. PowerLab Recording

The PowerLab was connected to a laptop via USB to record heartbeat rate and beat voltage in real-time in a digital format. This setup was adapted from previous experimental setups such as Burnett *et al.* (2013) and Pautsina *et al.* (2014). The PowerLab was set to record from the infrared sensors 1000 times per second, within the 20mV range and a mains filter was applied to reduce data noise via the 'Input Amplifier' settings. The output was in the form of a visual sine wave with voltage and time displayed on-screen. These results were also exported as raw voltage data into Microsoft Excel (Microsoft Corportaion, 2022) to better calculate changes in beat voltage which indicates beat volume.

5.3.5. Statistical Analyses

To test for differences in cardiac activity between the three treatment groups, the outputs were sub-divided into their phases. The 'baseline phase' consisted of the mean beat rate and voltage for the first minute of recording. The 'shock phase' consisted of the duration of arrythmia and bradycardia after the addition of a cue and the 'final phase' consisted of the mean beat rate and voltage for the last minute of recording. All analyses were carried out in R (R Core Team, 2020). See Figures 5.7 – 5.9 for examples of each identified cardiac response phase.

Differences in the changes of voltage (mV) and beat rate (beats per min) between cardiac phases and treatment groups were analysed using Friedman's tests to account for repeated measures. A paired technique was employed, using an individual Friedman's test for each treatment group to compare phases and also for each phase to compare treatment groups i.e. a total of 12 Friedman's tests were performed, each with Conover's post hoc to determine the source of any significant differences. One-way ANOVAs with post-hoc Tukey tests were used to analyse the difference between the shock phase durations for each treatment type, as repeated measures were not a concern here. This shock phase was distinguished by significant arrhythmia once the cue was added to the water. A Levene's test, testing for equality of variance,showed that the data were homoscedastic ($p > 0.05$). A Fisher's exact test was used to analyse the frequency of occurrence of a cardiac reaction to the cues for the 3 treatment groups.

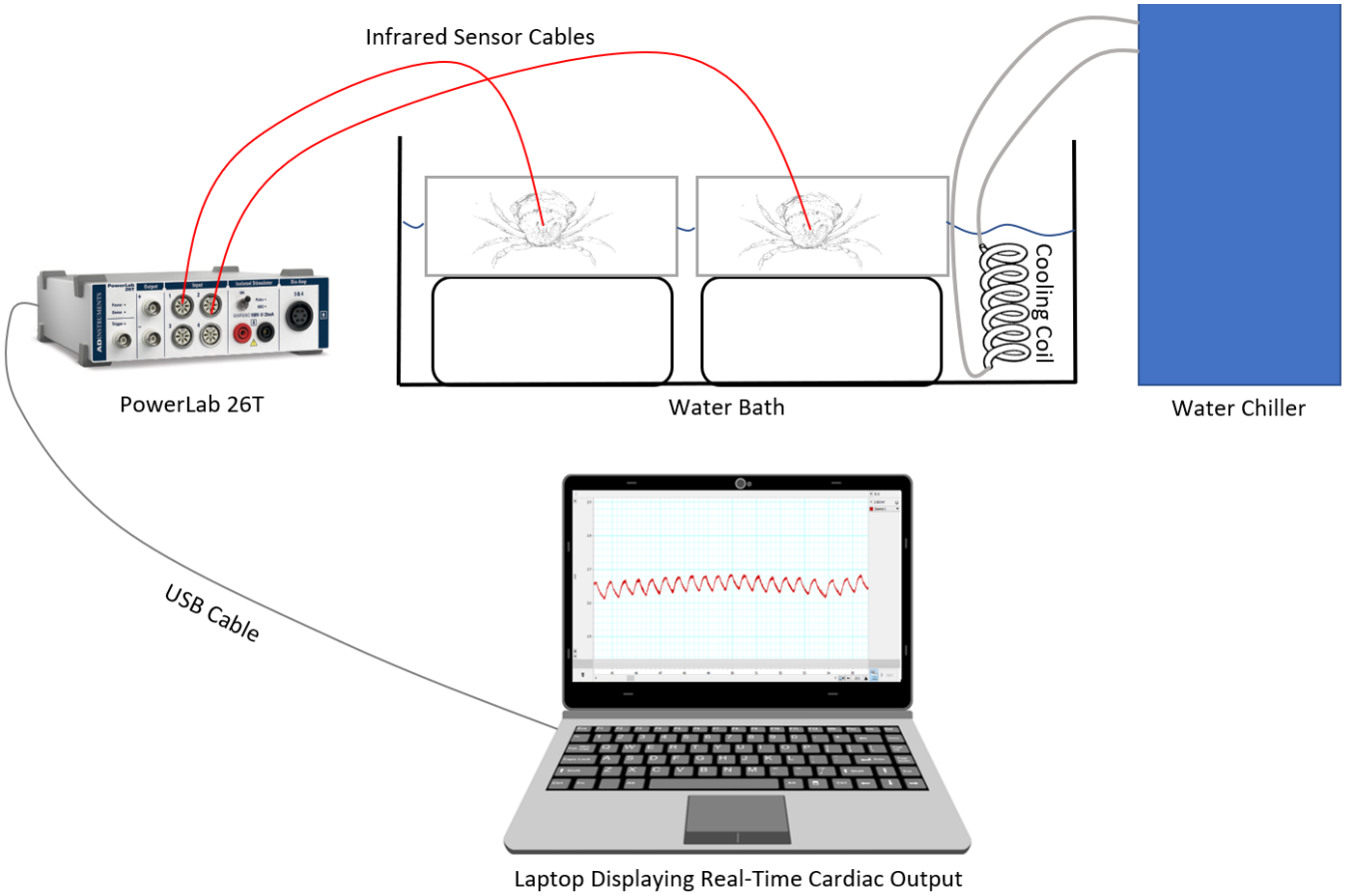

Figure 5.3 – Setup of infrared photoplethysmography equipment. The coil attached to the water circulator was part of a closed system and the water cooling was set to 12.5°C to achieve an ambient water bath temperature of 13°C.

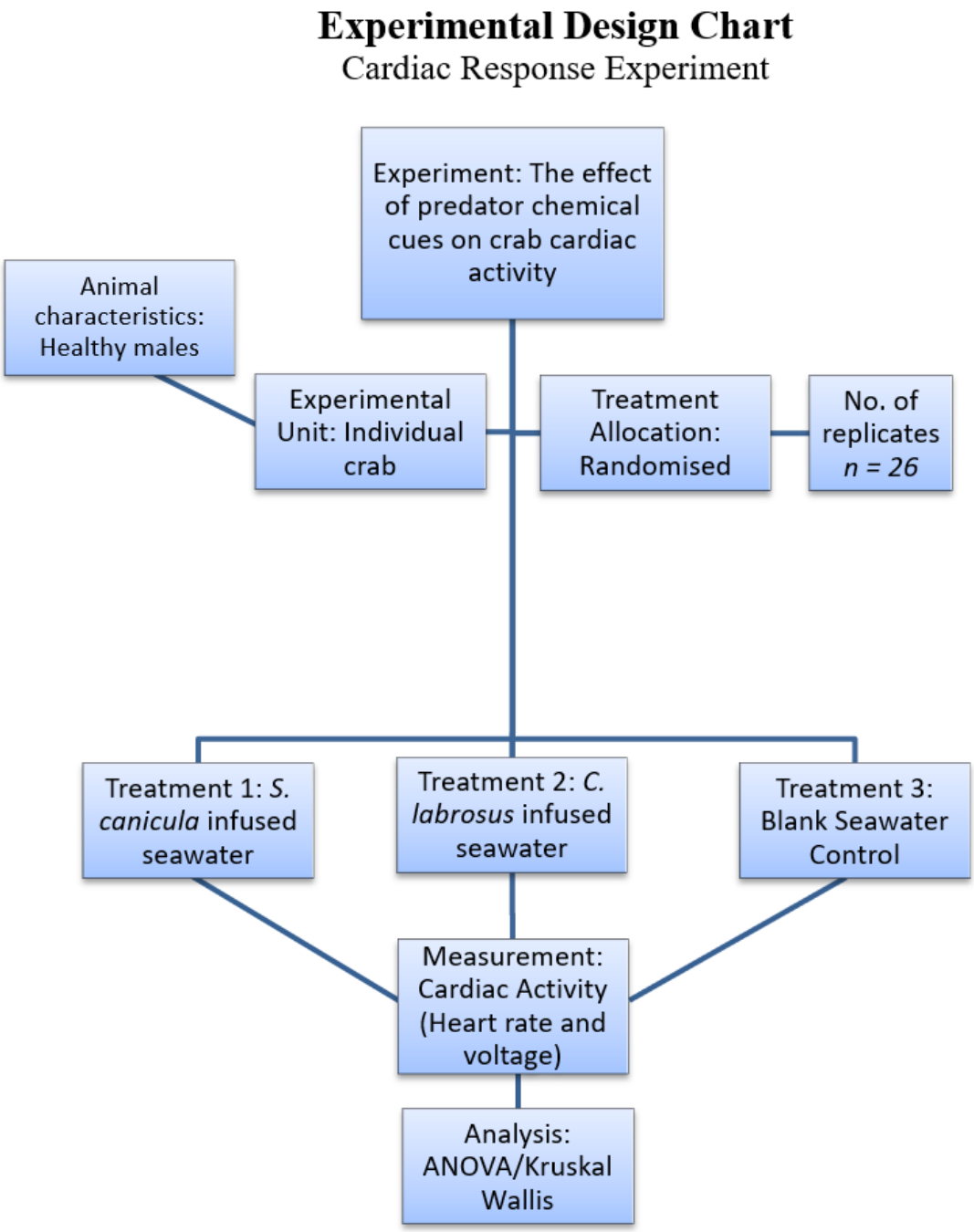

Figure 5.4 – Flow chart showing the experimental design. Animal characteristics, treatment allocation, experimental units, measurements, analyses used and individual treatment combinations are displayed.

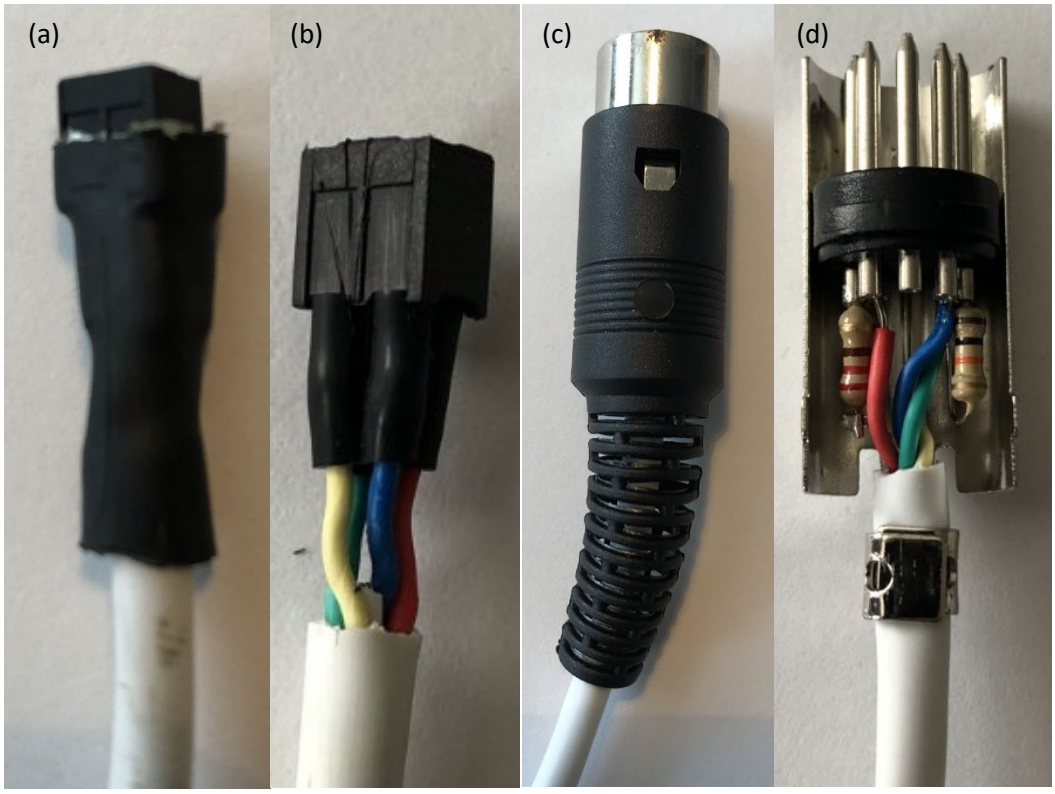

Figure 5.5 – Internal components of the infrared optical sensor cable – (a) Infrared optical sensor/coupler RPR220 soldered to 4 cores of the alarm wire, with heat shrink protection; (b) infrared sensor attached to wire, with wire cores exposed to show individual connections to the connector pins; (c) din pin connected to the same wire, with protective plastic cover; (d) din pin with protective cover removed, showing wire core connections and metal film resistors.

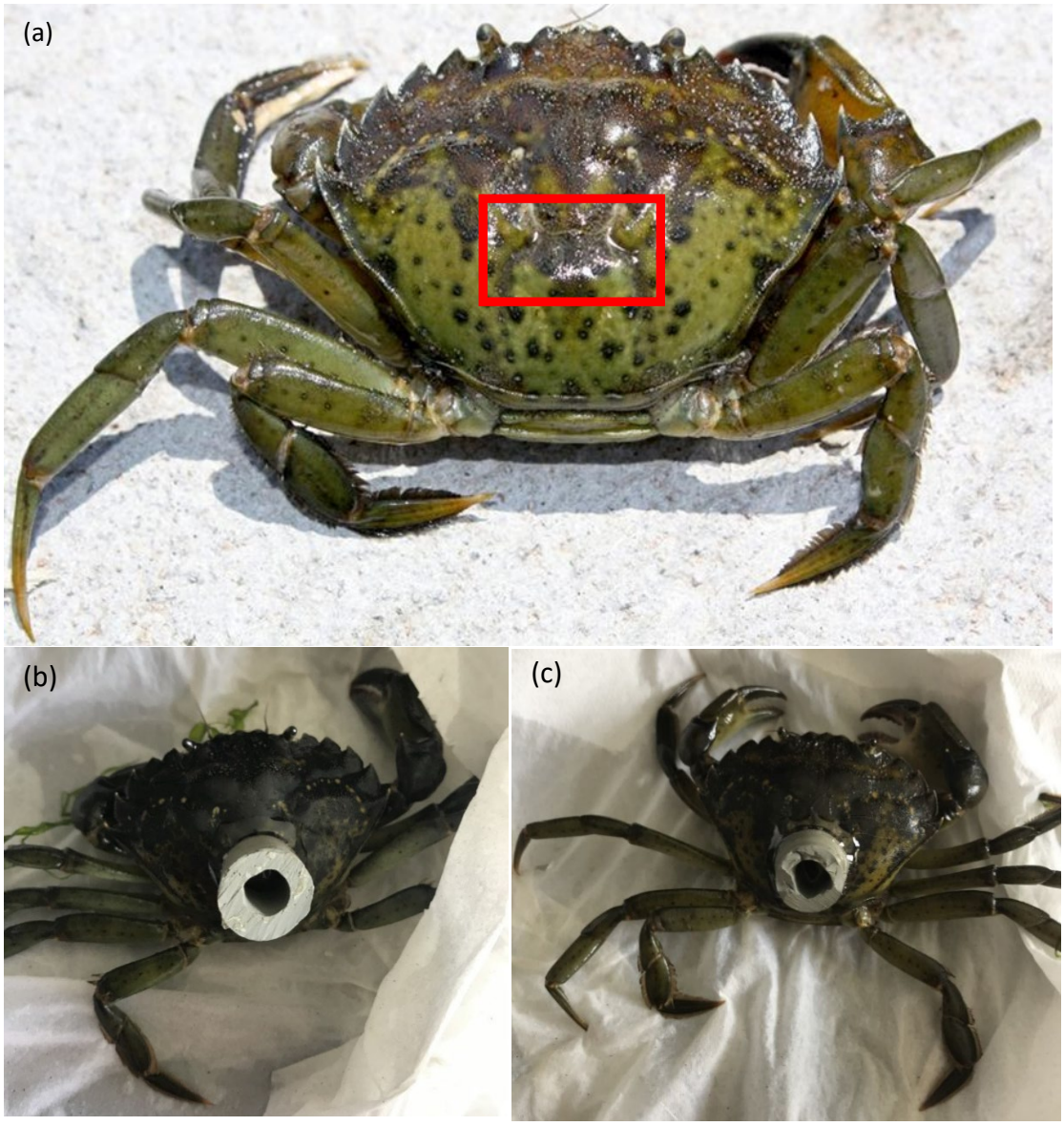

Figure 5.6 – (a) Image showing the underlying cardiac groove structure, highlighted by the red square. (b)+(c) Images showing the positioning of modified bungs over the 'cardiac groove' region of *C. maenas*' carapace, directly over the internal location of the main cardiac tissue. Sensors were additionally waterproofed using laboratory film and then slotted into these bungs before experiments began.

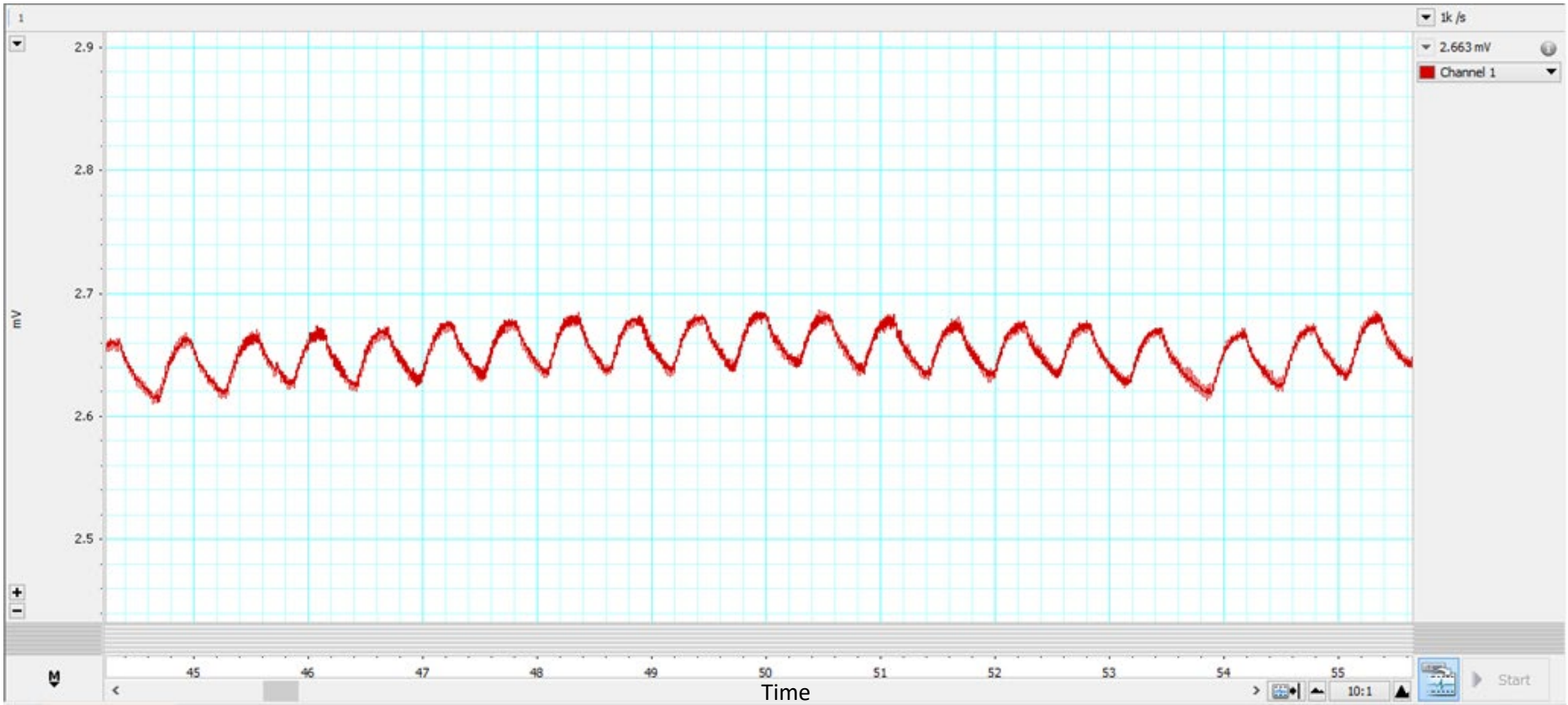

Figure 5.7 – A snapshot example of a LabChart output for the baseline cardiac phase, with voltage in mV on the y-axis and time in minutes and seconds on the x-axis. The sample rate is displayed in the top-right corner (1k/s).

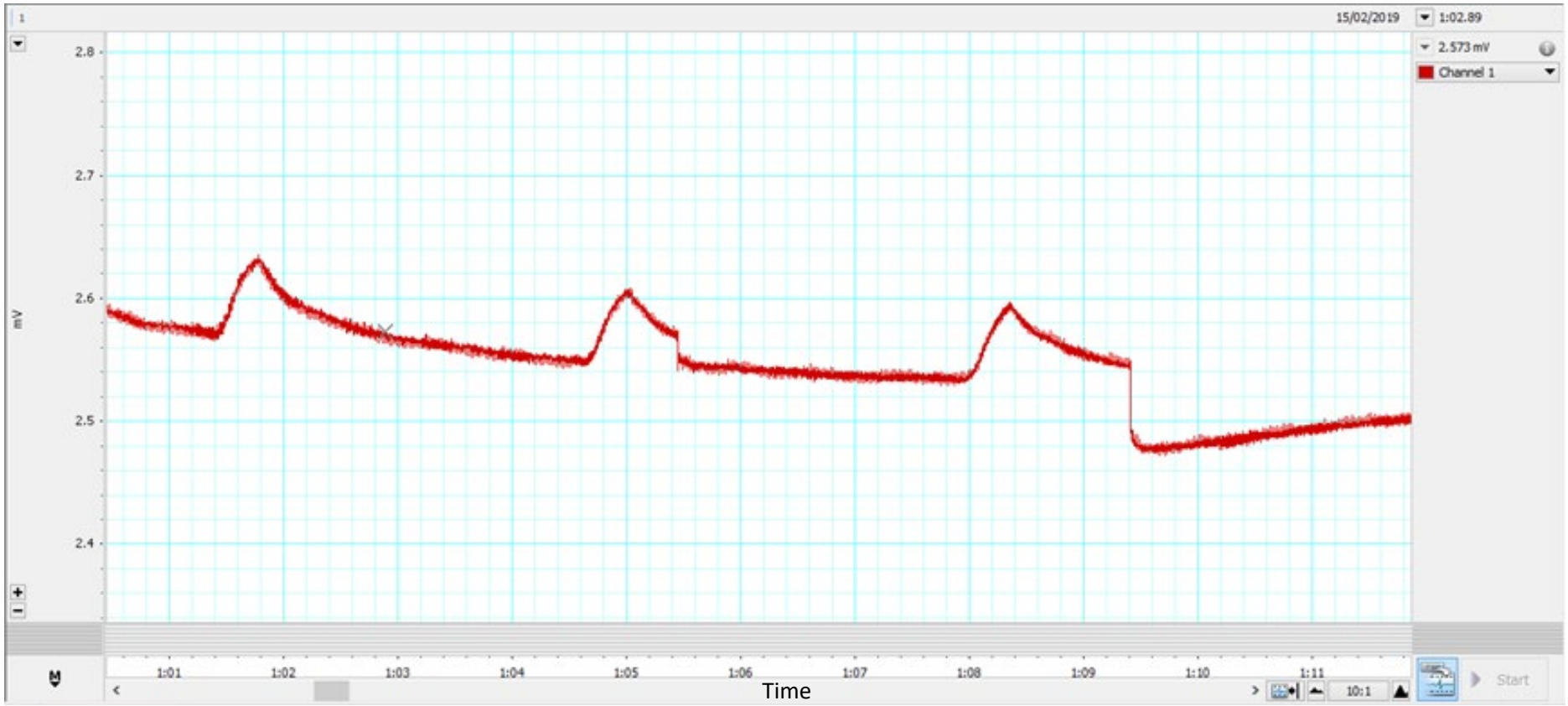

Figure 5.8 – A snapshot example of a LabChart output for the shock cardiac phase, with voltage in mV on the y-axis and time in minutes and seconds on the x-axis.

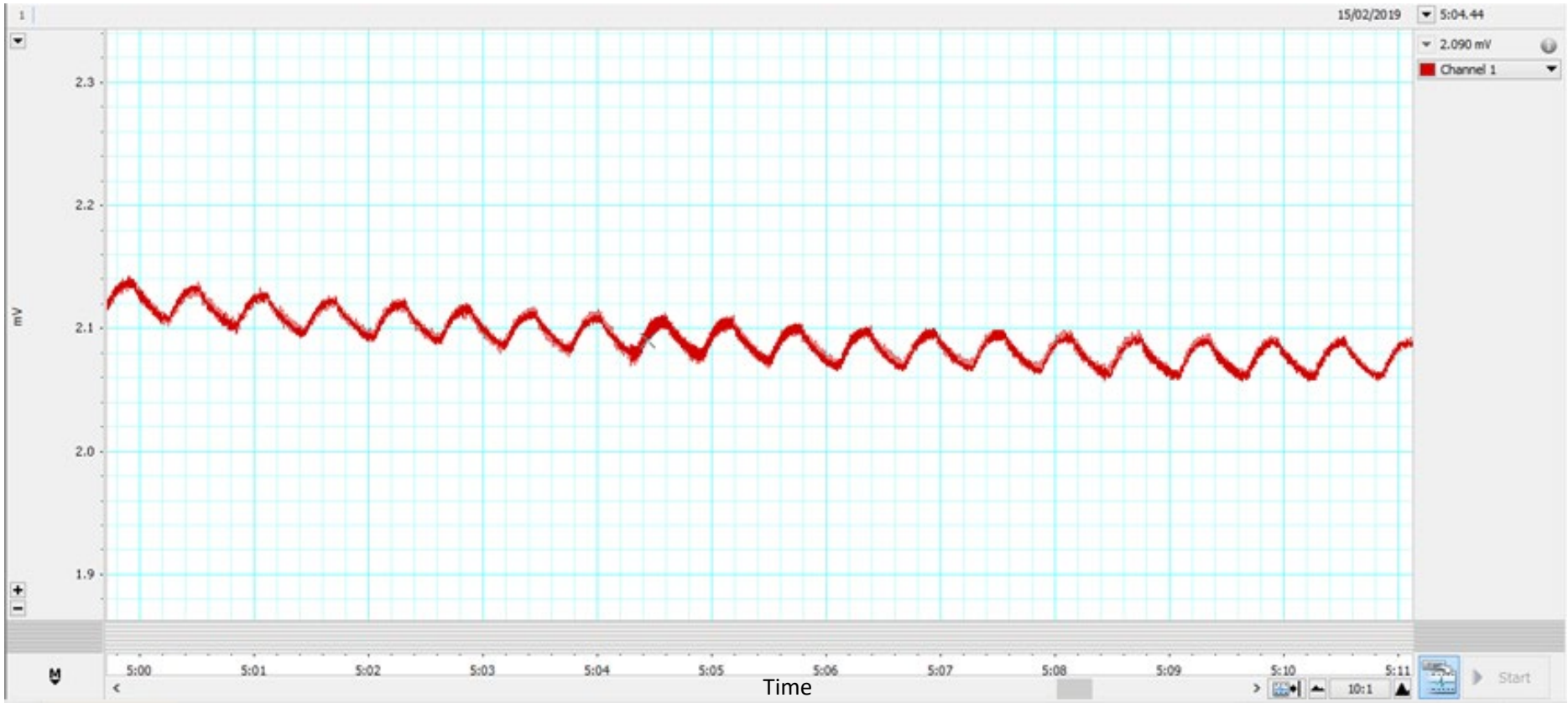

Figure 5.9 – A snapshot example of a LabChart output for the final minute cardiac phase, with voltage in mV on the y-axis and time in minutes and seconds on the x-axis.

5.4. Results

5.4.1. Voltage changes between treatment groups and cardiac phases

Crabs displayed the highest change in voltage between the baseline and shock phases in the presence of the dogfish chemical cue. This change was significantly higher than the response to the to the mullet cue ($T_{(2,50)}$ = 2.1, p<0.05), but not to the blank cue (p>0.05), see Figure 5.10. There were no further differences found in voltage change between treatment groups. Within each treatment group, the voltage change between the baseline and shock phase was significantly higher than between the other phases (all p < 0.05) and there were no significant differences in voltage change between the other phases (baseline - final min and shock – final min). See Table 5.1 for a matrix of these results. See Figure 5.11 for voltage changes between the phases within each treatment.

5.4.2. Heartbeat rate changes between treatment groups and cardiac phases

Between the baseline and shock phases, the dogfish and mullet cue treatment groups had significantly higher changes in heartbeat rate than the control treatment group ($T_{(2,50)}$ = 2.933, p<0.05 and $T_{(2,50)}$ = 3.488, p<0.05 respectively). There were no significant differences in voltage change between the dogfish and control treatment groups between these two cardiac phases. Within treatment groups, there were significant differences found in heartbeat rate change between the cardiac phases, see Table 5.2 for a matrix of these results. See Figure 5.12 for bpm changes between phases for each treatment.

5.4.3. Shock phase duration

C. maenas crabs had significantly different shock phase durations between chemical cue treatments ($F_{(2,75)} = 4.757$, $p<0.05$). Specifically, the Tukey test showed that crab shock phase duration was significantly longer when exposed to *S. canicula* compared to *C. labrosus* cues ($p <0.05$). Crab shock phase duration was significantly shorter in the *C. labrosus* treatment group compared to the control ($p <0.05$). Shock phase duration did not significantly differ between *S. canicula* and control treatments ($p>0.05$), see Figure 5.13.

5.4.4. Frequency of reaction to cues

Crabs displayed a cardiac reaction to the dogfish cue ~96% of the time (25 of 26 individuals). A similar reaction rate was found for the control cue, with a cardiac reaction being induce in ~92% of the treatment groups (24 of 26). The mullet cue only elicited a cardiac reaction in ~65% of the treatment group (17 of 26). The Fisher's Exact Test showed that crabs were significantly less likely to react to the mullet cue than the other two cues ($p <0.05$), see Figure 5.14.

Table 5.1 Significance of differences in voltage change between phases within each treatment group. Green highlighting represents significance, red represents non-significance.

Cue Treatment	Cardiac Phases	Baseline -Shock	Baseline – Final Min	Shock – Final Min
S. canicula	Baseline - Shock		$T_{(2,50)} = 3.054$ $p<0.05$	$T_{(2,50)} = 2.902$ $p<0.05$
	Baseline – Final Min	$T_{(2,50)} = 3.054$ $p<0.05$		$p>0.05$
	Shock – Final Min	$T_{(2,50)} = 2.902$ $p<0.05$	$p>0.05$	
C. labrosus	Baseline - Shock		$T_{(2,50)} = 4.299$ $p<0.05$	$T_{(2,50)} = 3.288$ $p<0.05$
	Baseline – Final Min	$T_{(2,50)} = 4.299$ $p<0.05$		$p>0.05$
	Shock – Final Min	$T_{(2,50)} = 3.288$ $p<0.05$	$p>0.05$	
Control	Baseline - Shock		$T_{(2,50)} = 2.335$ $p<0.05$	$T_{(2,50)} = 2.043$ $p<0.05$
	Baseline – Final Min	$T_{(2,50)} = 2.335$ $p<0.05$		$p>0.05$
	Shock – Final Min	$T_{(2,50)} = 2.043$ $p<0.05$	$p>0.05$	

Table 5.2 Significance of differences in heartbeat rate change between phases within each treatment group. Green highlighting represents significance, red represents non-significance.

Cue Treatment	Cardiac Phases	Baseline -Shock	Baseline – Final Min	Shock – Final Min
S. canicula	Baseline - Shock		$T_{(2,50)}$ = 4.027 $p<0.05$	$p>0.05$
	Baseline – Final Min	$T_{(2,50)}$ = 4.027 $p<0.05$		$T_{(2,50)}$ = 4.530 $p<0.05$
	Shock – Final Min	$p>0.05$	$T_{(2,50)}$ = 4.530 $p<0.05$	
C. labrosus	Baseline - Shock		$p>0.05$	$T_{(2,50)}$ = 2.877 $p<0.05$
	Baseline – Final Min	$p>0.05$		$T_{(2,50)}$ = 4.446 $p<0.05$
	Shock – Final Min	$T_{(2,50)}$ = 2.877 $p<0.05$	$T_{(2,50)}$ = 4.446 $p<0.05$	
Control	Baseline - Shock		$T_{(2,50)}$ = 4.813 $p<0.05$	$p>0.05$
	Baseline – Final Min	$T_{(2,50)}$ = 4.813 $p<0.05$		$T_{(2,50)}$ = 3.547 $p<0.05$
	Shock – Final Min	$p>0.05$	$T_{(2,50)}$ = 3.547 $p<0.05$	

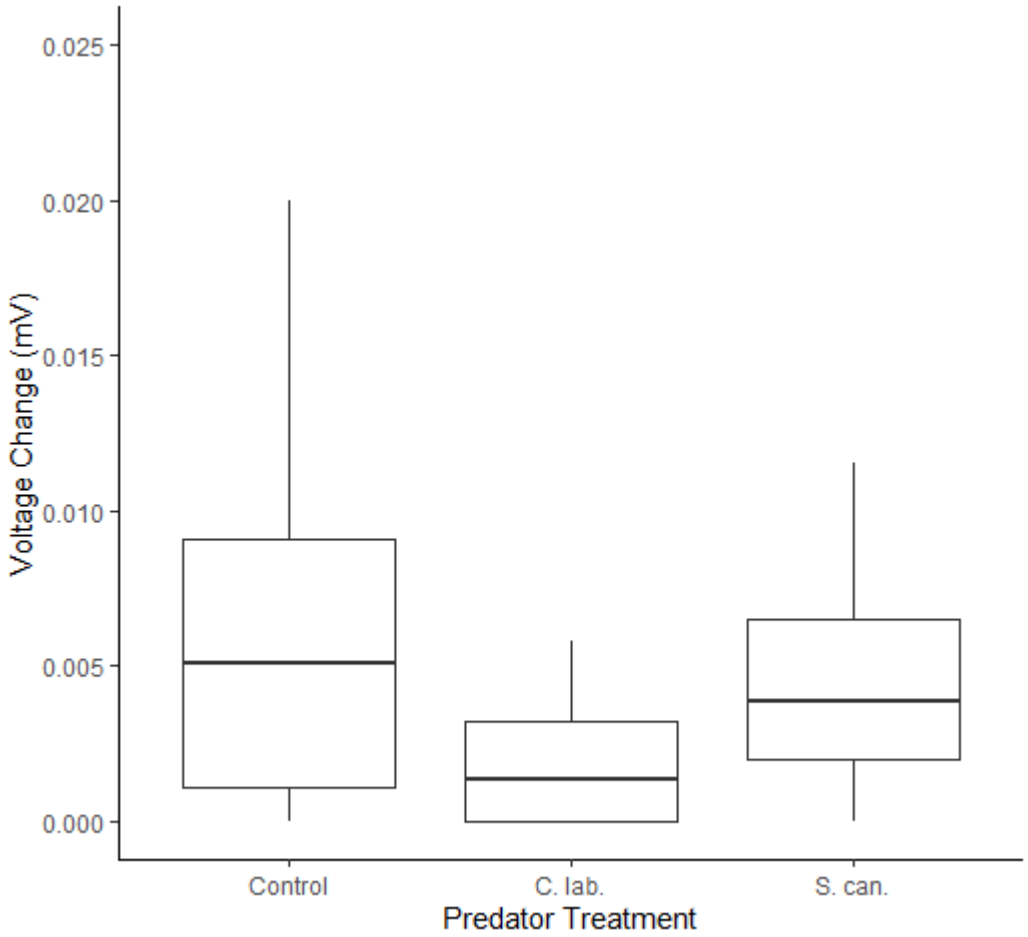

Figure 5.10 Boxplot of voltage change between baseline and shock cardiac phases across treatment groups. Cue treatment is displayed on the x-axis and voltage change is displayed on the y-axis.

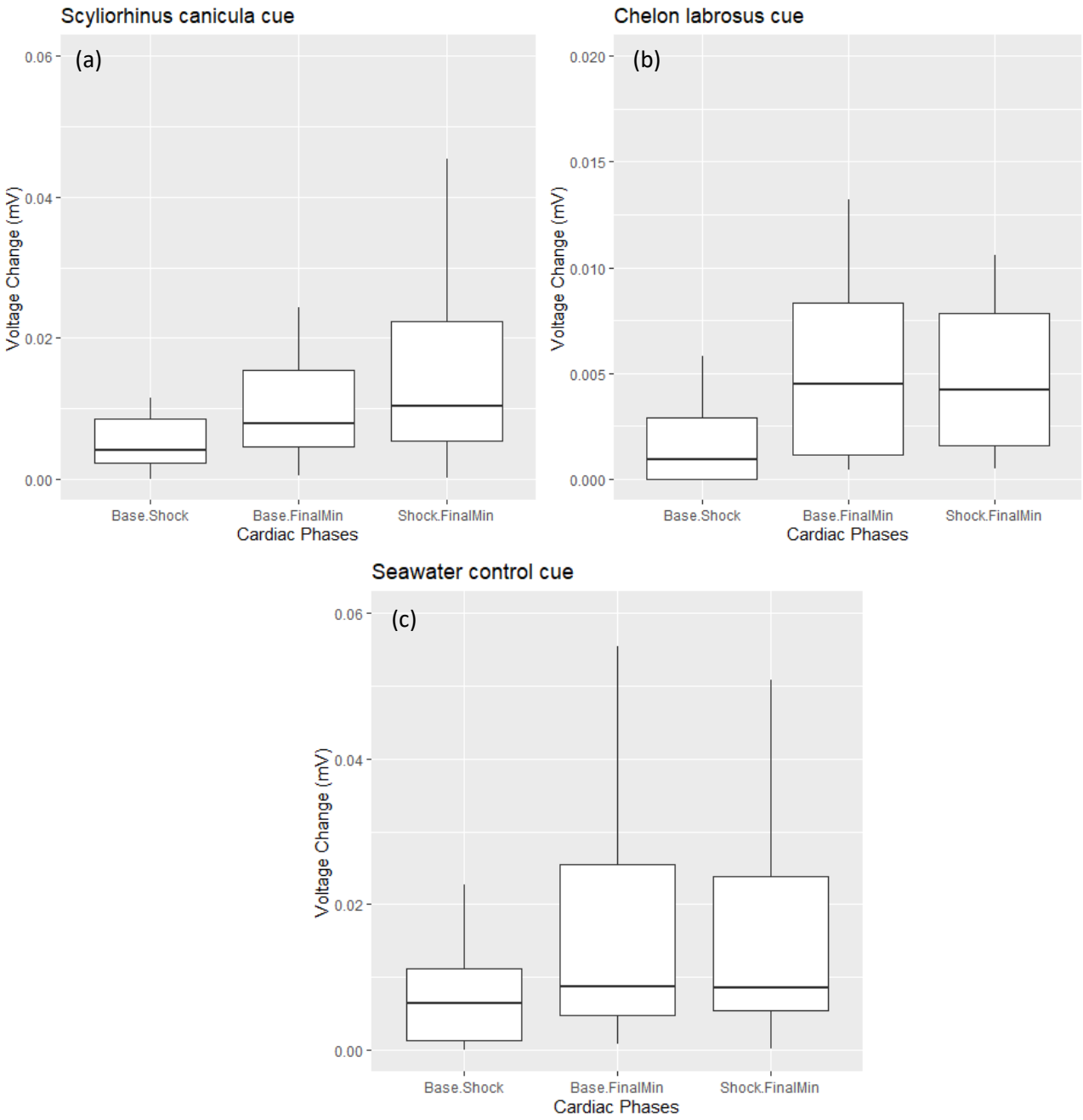

Figure 5.11 Changes observed in beat voltage of *C. maenas* between cardiac phases for each chemical cue. (a) voltage of crabs exposed to the cue of the predator, *S. canicula*. (b) voltage of crabs exposed to the cue of the non-predator, *C. labrosus*. (c) voltage of crabs exposed to a blank control cue of filtered seawater. Voltage change in mV on y-axes, cardiac phases displayed on x-axes and whiskers represent variation outside the upper and lower quartiles

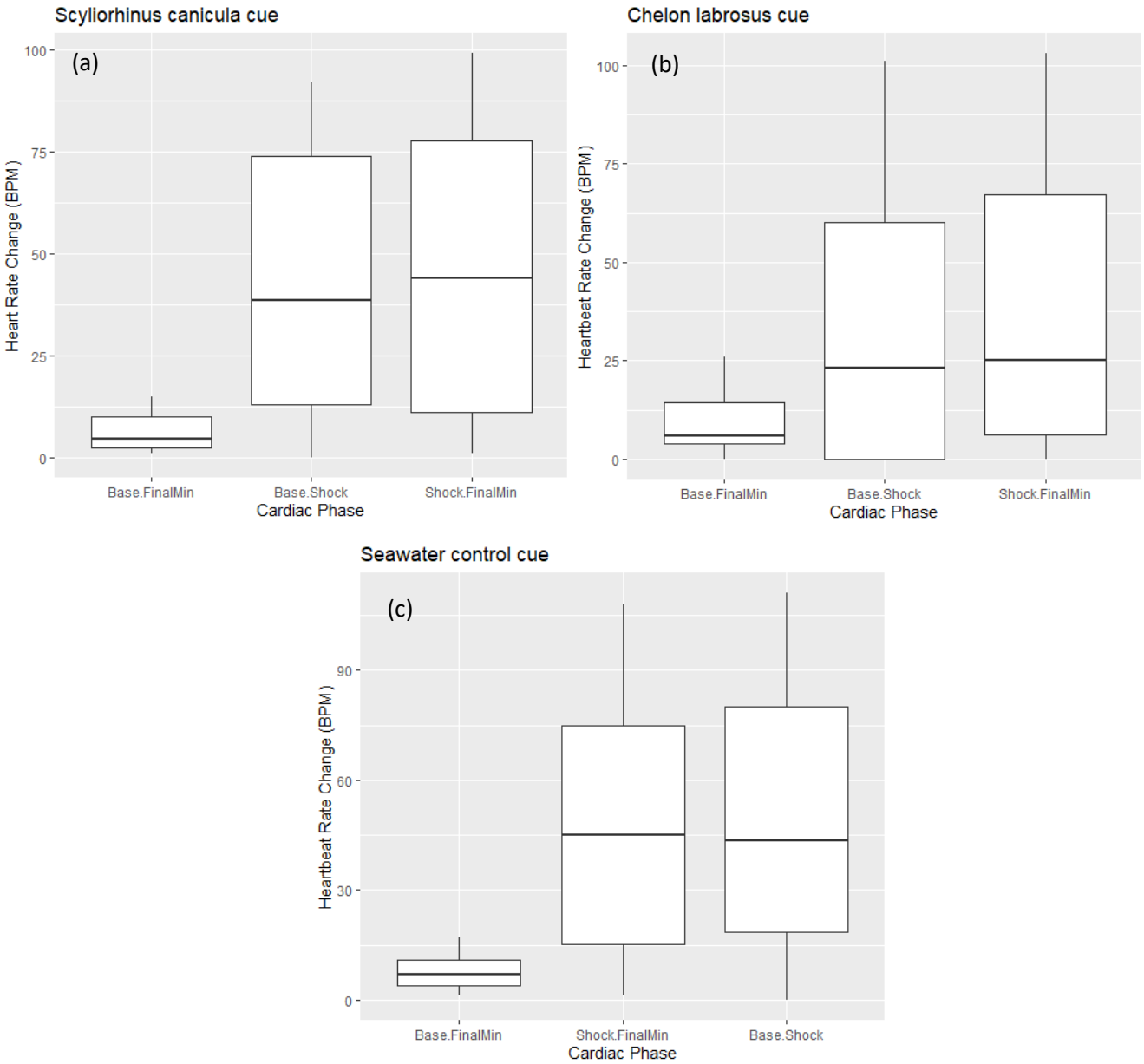

Figure 5.12. Changes observed in *C. maenas* heart rate between cardiac phases for each chemical cue treatment. (a) changes in heart rate for crabs exposed to the cue of the predator, *S. canicula*. (b) changes in heart rate for crabs exposed to the cue of the non-predator, *C. labrosus*. (c) changes in heart rate for crabs exposed to a blank control cue of filtered seawater. Heart rate change in BPM on y-axes, cardiac phases displayed on x-axes and whiskers represent variation outside the upper and lower quartiles

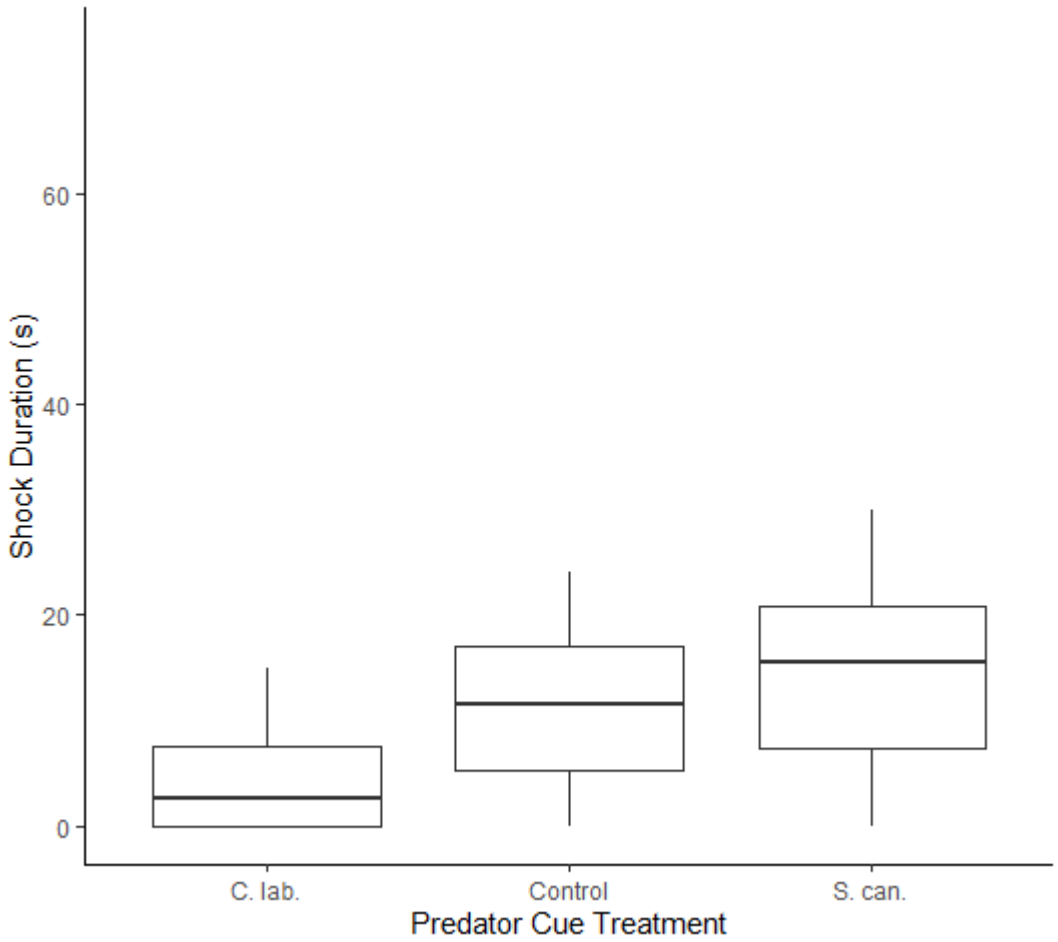

Figure 5.13 – Showing Shock phase duration across all predator cue treatments. . Duration in seconds that *C. maenas* crabs experienced cardiac shock (shock phase) when exposed to the three different predator treatment cues. Whiskers represent variation outside of the upper and lower quartiles.

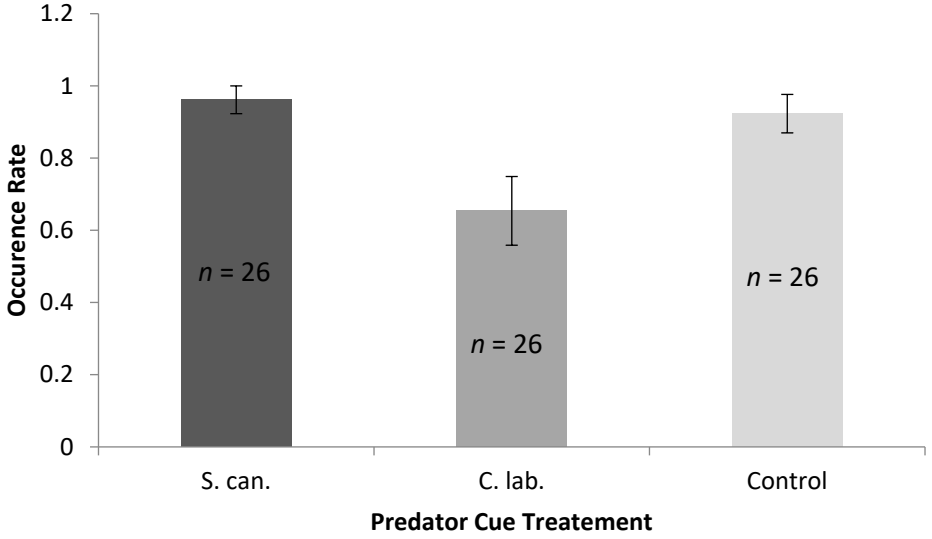

Figure 5.14Showing the rate at which crabs reacted to the treatment cues. Error bars represent standard error, occurrence rate on y-axis and predator cue treatments on x-axis. Crabs reacted significantly less frequently to the *C. labrosus* cue than the other two treatments.

5.5. Discussion

Here, the aim was to determine whether the cardiac response of *C. maenas* would differ based on perceived predation threat via chemical cue. It was hypothesised that crab cardiac activity would differ when present with a known predator cue vs a known non-predator cue. The results support this hypothesis, as crabs exposed to the *S. canicula* cue reacted more frequently, responded with a greater increase in beat volume and were in shock for longer than when exposed to the *C. labrosus* cue.

5.5.1. Animal physiology and observed cardiac activity

The results indicated that the crabs could distinguish between the mullet cue, a fish that was not going to pose a threat, and the dogfish (a known predator) and control (slight movement of water, a cryptic cue) cues, which presented a greater threat. While there would have been a slight movement of water from each cue, due to the nature of water leaving the syringes used to apply the cues, the control represented a cryptic cue as there were (to the best of my abilities) no substantial predator chemical cues present. These findings are supported by the feeding ecology of the cue species used. For example, *S. canicula* is a generalist predator that takes a wide variety of prey, though decapod crustaceans make up a significant portion of their diet (Henderson and Dunne, 1999; Martinho *et al.,* 2012). This also aligns with previous findings that olfactory cues are used to inform anti-predator decision making in decapod crustaceans (Dalesman and Inchley, 2008). Brachyuran crabs in particular can evaluate changes in water movement simultaneously with olfactory information (Zimmer-Faust *et al.*, 1995). The results of the current study suggested that the chemical cues in the water mediated the cardiac fluxes induced by the stimulus of water movement when adding the cue treatments.

The crabs reacted more frequently and were in shock for longer in response to the blank control vs the mullet cue. This may reflect the unknown/cryptic nature of the control cue, or due to background levels of chemical cues in the water, eliciting an anti-predator 'readiness' response in reaction to an unknown threat, as the actual voltage (beat volume), remained similar in both the control and mullet treatments. Readiness responses have been observed in behavioural studies in the form of escape posturing (e.g. Turesson *et al.*, 2009). The findings here suggested that when presented with a cryptic cue (water movement), brachyuran crabs were able to modulate their anti-predator response based on further sensory information provided by chemical cues. This allowed for the reduction of their response in the presence of a known no-predator cue and the amplification of their response in the presence of a known and/or an unknown predator. My results also suggest that *C. maenas* does not recognise *S. canicula* as any more of a threat than a cryptic cue.

There is previous evidence of decapod crustaceans being able to distinguish between predatory and non-predatory chemical cues (Rosen *et al.*, 2009). Where the current study differs is the recording of nuanced cardiac changes that would not necessarily be reflected in behavioural responses. This could be a potential function of the 'alternate response' recorded in crab cardiac activity (Canero and Hermitte, 2014).

5.5.2. The cost/benefit trade-offs of observed cardiac activity

The increased metabolic costs caused by fear of predation can significantly reduce animal fitness and survivability (Brown and Kotler, 2004; Trussell *et al.*, 2006a). In decapod crustaceans cardiac activity in is controlled autonomically (Shuranova *et al.*, 2006), with a distinct fight, flight and alternate response functionality when reacting to fearful stimuli (Canero and Hermitte, 2014). The results of the current study suggested that crab cardiac

activity was altered less frequently in response to the mullet cue, a known non-predator, and that crabs were in cardiac shock for a significantly shorter time when presented with mullet cue. While the initial cardiac arrythmia in response to the chemical can increase metabolic costs, the subsequent bradycardia (alternative response) when the crabs were exposed to the *S. canicula* and control cues is potential evidence of an autonomic response capable of 'pausing' increased metabolic costs until the threat is fully assessed.

These findings suggested that brachyuran crabs can autonomically delay, and even prevent, costly physiological responses to potential threats, based on olfactory cues. Additionally, these results imply increased crab fitness and anti-predator response can be influenced by autonomically controlled cardiac activity. Similar mechanisms have been observed in aquatic vertebrates in response to chronically high predation pressure, whereby the animals respond to predator cues based on 'background' and 'immediate' threat analysis in order to reduce over-stressing and over-reacting (Brown *et al.*, 2006). The findings here provide evidence that decapod crustacean fear responses are analogous to those found in higher order marine vertebrates and that their anti-predator response are more sophisticated than previously thought.

5.5.3. Elasmobranch electromagnetic sense and crab cardiac activity

Elasmobranch predators use their ampullae of Lorenzini, electro-sensitive, gel-filled pores for hunting (Freitas *et al.*, 2006). All of the changes in cardiac activity observed during our experiments were within the detectable range of elasmobranch predators, some of which can detect changes as small as 5-15 nanovolts (Kalmijn 1982; Fields 2007). Thus, the observed crab cardiac changes have the potential to alter elasmobranch predator hunting success by autonomically making their electromagnetic signature larger, smaller, or more cryptic (in the

case of arrythmia and bradycardia combined). This is not an active choice by the crabs, as it is the autonomic nervous system and musculature that controls the changes in their cardiac output (Canero and Hermitte, 2014), but it is evidence of a potential evolutionary arms race between brachyuran crabs and electro-sensitive predators.

5.5.4. Mesopredator suppression and ecological implications

Previous research has highlighted the importance of marine predator-prey interactions and the ecosystem services provided by marine predators, such as preventing mesopredator release and other cascading effects (Ritchie and Johnson, 2009; Brook *et al.,* 2012). In marine systems, the subclass elasmobranchii contains a significant number of important keystone predator taxa, such as sharks, whose removal precipitates 'fear-release' in their respective ecosystems (Frid *et al.*, 2008). Despite their ecological importance, these important predators have been persecuted globally and the their extirpation has caused ecosystems to shift into less favourable ecological states as mesopredators are released (Prugh *et al.*, 2009). The results of the current study suggested that these animals have the ability to not only alter mesopredator (crab) behaviour, but that they might also directly impact prey physiology, altering prey fitness and metabolic cost. These results contribute to the scientific body of knowledge concerning the regulatory marine ecosystem services provided by elasmobranch predators by highlighting some of the physiological changes caused by fear of predation that precipitate anti-predator behaviour in brachyuran crabs.

Chapter 6

General Discussion

6.1. Marine Ecosystem Service Provision by Predator-Prey Interactions

The findings of the current thesis highlight the importance of predator-prey interactions in the provision of marine ecosystem services. My results provide further evidence that multiple elasmobranchs within a trophic guild act similarly as transient keystone species (*sensu* Barrios-O'Neill *et al.,* 2017). They all function to suppress the trophic cascades precipitated by fear released mesopredators, whereby mesopredators suppress habitat-forming-species' recruitment, such as mussels and oysters (Campbell et al., 2019; Christie et al., 2020; Kulp and Peterson, 2016; Plass-Johnson et al., 2010; Reimer and Tedengren, 1997). Such mesopredator suppression can be an important ecosystem service through indirectly enhancing basal species recruitment (Gordon et al., 2015; Letnic et al., 2009; Nifong and Silliman, 2013; Terborgh and Davenport, 2020). Furthermore, keystone predators play an active role in structuring marine ecological communities, providing trophic stability (Boaden and Kingsford, 2015; Hammill et al., 2015; Hein and Gillooly, 2011) through the maintenance of a landscape of fear (Bleicher, 2017; Gaynor et al., 2019; Laundré et al., 2010).

Raja clavata and *Scyliorhinus stellaris,* occupy the same trophic guild, but are evolutionary distinct, and displayed similar rates of mesopredator foraging. This finding suggests guild redundancy at an ecosystem scale (Lawton and Brown, 1994). The guild effects on mesopredator foraging can support increased biodiversity through niche maintenance, bolstering ecosystem resilience (Naeem and Li, 1997; Ulanowicz, 2018; Biggs *et al.*, 2020). This redundancy can also dampen anthropogenically induced ecosystem cascades due to ongoing extinction events (e.g. Liu *et al.*, 2016 Sanders *et al.*, 2018).

This thesis demonstrated that marine elasmobranch predators can alter the physiological responses of prey species non-consumptively (cardiac response). This highlights the potential effects of a functioning landscape of fear on the individual, physiological level (Wirsing *et al.*, 2021). The crab cardiac responses support the hypothesis that the 'alternative response' in decapod cardiac physiology, associated with tonic immobility, is an adaptation to increase survivability during predation (Giannico *et al*., 2014; Maus *et al*., 2019). This fear induced alternate response has an associated physiological cost (O'Connor *et al.*, 2007). These fear induced costs can lead, over time, to reduced fitness and even cause death of prey species (Preisser *et al.*, 2005; Schmidt and Kuijper, 2015). This highlights the contribution of predator induced stress (within a fear landscape) in regulating the behaviour and fitness of mesopredators and ultimately ecosystem service regulation. For example, the results of this thesis show that the suppression of mesopredator feeding caused by predator induced stress is an ecosystem service as it can reduce the overgrazing of basal species and can mitigate the effects of mesopredator release, as found in previous studies(Berger and Conner, 2008; Brook *et al.,* 2012; Gordon *et al.*, 2015). The changes in population dynamics caused by such mesopredator suppression are able to then filter upwards, altering community structure (Menge, 1995; Wirsing *et al.*, 2008; Catalán *et al.*, 2021).

Furthermore, the results of this thesis demonstrated that native fear-released mesopredators can have similar functional responses to those of invasive species, notably a Type II functional response, which is considered ecologically destabilising (Barrios-O'Neill *et al.*, 2016; Dickey *et al.,* 2018; Joyce *et al.*, 2019; Cuthbert *et al.*, 2021). These results suggest that fear-released landscapes should be considered with the same management concern as those with invasive species (where fear released species act as invasive). The reduction in

the fearscape is a form of ecosystem degradation, with possible mitigation being the conservation and enhancement of keystone predators. The loss of such keystone predators across Europe, such as the extirpation of elasmobranchs in the Aegean (Zogaris and De Maddalena, 2014; Damalas *et al.*, 2021) and the stock collapse of the flapper skate (Garbett *et al.*, 2021), indicate the timeliness of my work and a potential recovery pathway for environmental management. My results provide multiple lines of evidence that demonstrate how the maintenance of a trophically complex fearscape is critical for marine ecosystem service provisioning. While my findings are not prescriptive, and further research is needed, they support the case for transient keystone predators being a potential tool for conservation and ecosystem management (Ritchie and Johnson, 2009; Sergio *et al.*, 2008; Caro, 2010; Ritchie *et al.*, 2012).

The research presented in this thesis highlights the importance of predator-prey interactions in ecosystem regulation, a major component of more holistic research, and one which requires more quantitative research (Rodriguez, 2017), and suggests that fear itself should be considered as an environmental factor influencing ecological communities. While marine systems remain relatively more heterogenous in their predator regimes than terrestrial systems, similar pressures from defaunation and overexploitation are leading to regime shifts (Ferretti et al., 2010; Dirzo *et al.*, 2014; McCauley *et al.*, 2015; Young *et al.*, 2016; Pacoureau *et al.*, 2021). For a more comprehensive understanding of these regime shifts, a holistic view, incorporating food-web dynamics with other environmental factors is suggested (sensu Conversi *et al.*, 2015).

Furthermore, my research involved tri-trophic chain experiments which used adult elasmobranchs over 1m long, while similar previous predator-mesopredator-bivalve chain

experiments have used smaller species such as crabs and fish, focusing on intertidal communities (Grabowski, 2004; Plass-Johnson *et al.*, 2010; Macreadie *et al.*, 2012; Kulp and Peterson, 2016). This is likely due to the difficult nature of recording large marine predator behaviour and the increased logistics involved compared to terrestrial research (Steele *et al.*, 1989; Beger *et al.*, 2010; Heupel *et al.*, 2014; Ferreira, 2017). The success of my research highlights the importance of overcoming these logistical issues to achieve more holistic assessments of marine predator-prey interactions.

6.2. Ecological Management, Conservation Policy, and Strangford Lough

The findings presented here provide evidence for the importance of fear landscapes in local marine ecological management. As described in Chapter 1, there is evidence of a regime shift in the locality of Strangford Lough caused by the degradation of *Modiolus modiolus* mussel reefs and the extirpation of large keystone predator such as the elasmobranch *Dipturus intermedia* (Barrios-O'Neill *et al.,* 2017). Potentially, the reintroduction of elasmobranchs to Strangford Lough could precipitate a trophic cascade, supporting horse mussel recruitment through suppression of mesopredator foraging (Beukema and Dekker, 2014; Nifong and Silliman, 2013; Van der Heide et al., 2014). Furthermore, the results of this thesis support the transient keystone concept, whereby bivalve reef recovery due to keystone predator effects could reach a threshold after which predator effects would be dampened by habitat complexity and the trophic cascade would be maintained by the mussel reef itself (Grabowski, 2004; Barrios-O'Neill *et al.*, 2017). In the context of the

degraded *M. modiolus* reefs in Strangford Lough, this suggests that not only top predators, but also transient keystone species such as *R. clavata* and *S. stellaris* could be utilised to achieve ecosystem management goals and facilitate the recovery of these important reef communities which host high biodiversity (Ulster Wildlife Trust, 2012).

Based on the evidence presented in this thesis, it is recommended that a holistic approach to ecological management is employed in Strangford Lough. It is recognised that the Department of Agriculture, Environment and Rural Affairs has already begun to adopt more holistic management styles, assessing habitats and biotopes as well as priority species (NIEA, 2010; McKeown, 2020). The findings of this thesis suggest that there is trophic overlap amongst native elasmobranchs, and that multiple species can provide the same ecosystems services, such as mesopredator suppression. Rearding the ecological management of Strangford Lough, these findings support the recommendation that the populations of species such as *S. stellaris* and *R. clavata* should be bolstered, or encouraged to return to sites of extirpation, to enhance ecosystem stability and resilience. Previous research has shown that this should be assessed on a site-specific basis using adaptive management techniques (Fazey *et al.*, 2004; McKeown, 2020).

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