Exploring the Past, Present, and Future of Predator-Prey Interactions Between Crabs and Their Gastropod Prey

by

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Abstract

Interactions between predators and prey play an important role in structuring their communities and shaping evolution. However, human-induced climate change has the potential to influence both predators and prey and disrupt their interactions. The fossil record provides an enormous resource to investigate how both past and current climate change has affected organisms, their interactions, and ecosystems. In particular, scars left on prey by failed predatory attacks provide an excellent record, and often the only evidence, of predator-prey interactions in both modern and fossil ecosystems. However, as these injuries, known as repair scars, are records of failed rather than successful attacks (with successful attacks destroying the prey), it can be difficult to interpret whether repair scars signal overall attack rates, or the success/failure rate of the predator. Furthermore, the presence of repair scars can be affected by the structural integrity of the prey's defenses, such as a gastropod shell, as well as prey selection by the predator. Here, shell-crushing crabs and their gastropod prey were used as a model system for exploring potential relationships between prey defenses, prey selection, and repair scars in the past, present, and possible future. Specifically, the goals were: 1) to use modern experiments to understand how prey defenses are affected by ocean acidification, a major by-product of carbon dioxide emissions, 2) to test patterns of prey selection by crabs, and 3) to then examine how patterns of repair scars in gastropods manifest through both space and time.

Along the west coast of North America, crabs such as *Cancer productus* and their gastropod prey are key members of rocky intertidal communities. Exploration of the potential mechanisms by which human activity might disrupt these predator-prey interactions could provide insights to help protect these critical species and their relationships. In Chapter 2, I tested how gastropod shells are affected by both ocean acidification and predation cues in the gastropods *Tegula funebralis* and *Nucella ostrina*. After exposure to decreased seawater pH and/or predation cues for six months, both shell growth and strength in *T. funebralis* was drastically reduced. However only shell strength, and not growth of *N. ostrina* was impacted by low pH treatments, and not as severely as *T. funebralis*. Examination of shell composition and microstructure of both species in Chapter 3 used microCT scans, XRD analysis, and SEM imaging, indicated that the loss of shell strength was from dissolution of the outermost shell layer in both species, with the microstructural arrangement of *T. funebralis* shells likely causing more severe dissolution than observed in *N. ostrina*. Patterns of crab (*C. productus*) prey selection between three species of the gastropod *Nucella* were examined in Chapter 4 to understand how crabs attack and select prey. The experiment revealed that crabs are most likely to attack the first gastropod they detect, with a preference for the largest species most likely driven by their inability to always recognize smaller prey. I then explored patterns of repair scars in *T. funebralis* both geographically along the modern west coast of Canada and the U.S. (Chapter 5), as well as temporally between the Late Pleistocene and modern of southern California (Chapter 6). By measuring the size at which repair scars occur, I demonstrate that it is possible to distinguish between repair frequency and predator success, allowing more accurate comparisons of predation between samples. Crab predation in the modern also showed strong regional, but not latitudinal, variation along the west coast, with the lowest number of attacks in southern California. Furthermore, comparisons of modern and fossil repair scars in southern California indicated that there are fewer crab attacks today, suggesting that crab populations may already be affected by human activity. By studying how prey defenses, prey selection, and repair scar systems manifest, we can explore how predator-prey relationships have changed both in the past and present, and how they may continue to change due to our current climate crisis.

Preface

Chapter 2 of this thesis has been published as: Barclay, K. M., B. Gaylord, B. M. Jellison, P. Shukla, E. Sanford, & L. R. Leighton. 2019. Variation in the effects of ocean acidification on shell growth and strength in two intertidal gastropods. *Marine Ecology Progress Series*, 626:109 – 121. DOI: 10.3354/meps13056. I was responsible for all data collection, analyses, and composition of the manuscript and associated tables and figures. B. Gaylord, E. Sanford, B. M. Jellison, and L. R. Leighton assisted with the study design. P. Shukla instructed and assisted with data collection. E. Sanford, B. M. Jellison, and L.R. Leighton assisted with analyses. All authors assisted in compiling the manuscript. L.R. Leighton was the supervisory author.

Chapter 4 of this thesis has been previously reviewed as: Barclay, K. M., C. R. Sinclair, & L. R. Leighton. Factors influencing crab preference between three similar gastropod species. I was responsible for all data collection, analyses, and composition of the manuscript. C. R. Sinclair and L. R. Leighton assisted with data collection and study design. All authors assisted in compiling the manuscript. L. R. Leighton was the supervisory author. The manuscript has been resubmitted to the *Journal of Experimental Marine Biology and Ecology* as a new submission, with all reviewer concerns addressed and included.

Dedication

For my sister, Danielle.

Your courage, perseverance, and unyielding strength in the face of terrible hardships inspires me daily. I am a better, stronger person and scientist because of you.

In loving memory of my grandmother, Marion Barclay.

A fellow writer and kindred spirit who would have been the first person to read this work from cover to cover.

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I would like to thank my supervisor, Dr. Lindsey Leighton, for his support, encouragement, and advice. It has been a pleasure to work for him over the past several years, and I would not have decided to pursue this degree, or become the scientist I am today, without his support, patience, guidance, and thorough feedback. I feel lucky to have had such a caring and involved supervisor. I am also eternally grateful for his trust and flexibility in letting me pursue this degree long-distance, which allowed me to spend more time at home with my family. I hope that I have made him proud, even if I continue to split infinitives.

I would also like to thank the members of my supervisory committee, Drs. Brian Gaylord, and John-Paul Zonneveld for their support, advice, and feedback. I am so grateful to Dr. Gaylord and his students for welcoming me into their lab, and providing me resources, support, and guidance. Dr. Gaylord's kindness, guidance, and understanding during a troubling family crisis made a very strong impression in deciding the kind of mentor I'd like to be.

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Finally, I owe the majority of my success to my family and friends. I will forever be grateful to my husband, Chris Beckett, for his infinite patience and support, especially while I lived out of a suitcase and moved to Edmonton, and then California, during the first years of our marriage. His kindness and caring have held me together when my world was falling apart. I am also thankful to my parents, Glenn and Shirley, for their continued support and encouragement throughout my education, and for always providing me the opportunity to pursue my passions, as well as a shoulder to lean on. My sister, Danielle, is the single most resilient human I have ever met, and I am thankful just to call her my sibling and to learn from her example how to make a difference in the world. I also thank my in-laws, Ken and Sherril, my extended family, and wonderful circle of friends for their interest, encouragement, and support through the years.

As a biologist, I am constantly falling in love with the animals I meet. The strength of connections we can derive from our animal friends is one of my favourite things about my field of study. I must therefore acknowledge two animal friends who have helped me complete my studies while working from home. I credit my cat, Widget, for helping me stay focused when studying for my candidacy exam. I am convinced he is the reason I passed. And I must also give thanks for my cat May, who has helped to heal my broken heart after we lost Widget unexpectedly. She made it a little easier to work from home again, and reminded me to take regular play breaks while I wrote my dissertation.

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Chapter 1

Introduction

Predation is an important component of most ecosystems. Predators are known to control the populations, distributions, and behaviour of their prey (Menge 1976; Bertness 1977; Markowitz 1980; Geller 1982*a*; Boulding and Hay 1984; Fawcett 1984; Palmer 1985, 1990; Menge and Sutherland 1987; Appleton and Palmer 1988; Marko and Palmer 1991; Vadas et al. 1994; Behrens Yamada and Boulding 1996, 1998; Kats and Dill 1998; Chivers and Smith 1998; Jacobsen and Stabell 2004; Bertness et al. 2004; Bourdeau 2009, 2010*a*; Mach and Bourdeau 2011; Gravem and Morgan 2017), and the indirect effects of predation on both their prey and ecosystems in general have been widely demonstrated over the past few decades (Paine 1969*a*; Holt 1977, 1984; Trussell et al. 2003; Hull and Bourdeau 2017). The presence of predators can also cause prey to respond plastically by changing their morphology to forms that are more resistant to predation (Palmer 1985; Appleton and Palmer 1988; Bourdeau 2009, 2010*a*, 2011, 2012; Pascoal et al. 2012). Differential mortality of prey forms can also lead to selection for, and the evolution of, more predator resistant body forms in prey (Vermeij 1977*a*; Palmer 1979; Vermeij 1982*a*, 1987, 1993, 1994; Dietl and Kelley 2002; Kelley et al. 2003). However, compared to the lifetime of an organism, predation events are fleeting. And while it may be challenging to observe such brief predation events in modern ecosystems, it is impossible to do so in the fossil record.

Traces of predation left on prey organisms, such as scars on shells, often provide the only direct evidence of predation in both modern and fossil ecosystems. But one of the biggest challenges in using such traces to study predation is that these marks, known as repair scars, represent failed rather than successful attacks, which can make accurate interpretation of predation rates and predator success challenging (Vermeij et al. 1981; Vermeij 1982*a*; Alexander and Dietl 2001, 2003; Leighton 2002; Dietl and Kosloski 2013; Molinaro et al. 2014; Budd and Mann 2019). Furthermore, the presence of a scar is also influenced by both the structural integrity of the prey's defenses in resisting predation, and prey selection by the predator. Critically, in marine systems, prey defenses are often made of calcium carbonate ($CaCO_3$), which is sensitive to ocean acidification caused by increases in atmospheric carbon dioxide, as is the case today. Ocean acidification (OA) has the potential to disrupt predator-prey interactions by weakening prey defenses and changing the success rates of predators (Gaylord et al. 2011; Amaral et al. 2012; Coleman et al. 2014; Kroeker et al. 2014; Sanford et al. 2014*a*; Wright et al. 2014; Fitzer et al. 2015). In the follow dissertation, I use predator-prey relationships between crabs and their gastropod prey as a model system for studying how ocean acidification, prey selection, and repair scars can be used to explore patterns of predation through the past, present, and possible future.

Durophagy (shell-crushing) has been a common method of predation for most of the Phanerozoic (Vermeij et al. 1981; Vermeij 1983; Leighton 2002; Alexander and Dietl 2003). In particular, the rise of shell-crushing crabs in the Mesozoic has been attributed to the evolution and proliferation of antipredatory adaptations and lineages of molluscs as part of the Mesozoic Marine Revolution (Vermeij 1977*a*; Schweitzer and Feldmann 2010). Shell-crushing crabs are still important predators in modern marine ecosystems, where they are known to control the populations, distributions, morphology, and behaviours of their prey (Bertness and Cunningham 1981; Geller 1982*b*; Boulding and Hay 1984; Palmer 1985, 1990; Appleton and Palmer 1988; Marko and Palmer 1991; Schindler et al. 1994; Vadas Sr et al. 1994; Behrens Yamada and Boulding 1996; Jacobsen and Stabell 2004; Bourdeau 2009, 2011, 2012; Edgell 2010; Mach and

Bourdeau 2011; Lord and Barry 2017), and serve as keystone taxa that indirectly influence the rest of their ecosystems (Trussell et al. 2003; Bertness et al. 2004; Hull and Bourdeau 2017). Prey defenses are therefore integral for resisting durophagous predation by predators such as crabs.

While some prey develop elaborate ornament that might inhibit gape-limited predators by making them too large to handle, ultimately, the strength of any defensive structure is the most important metric for resisting durophagy (Alexander 1986). If defensive structures can be broken or removed, the prey will still be vulnerable (Whitenack and Herbert 2015). Changes to the carbon cycle, such as ocean acidification, therefore have the potential to interfere with the production and maintenance of these structures (Doney et al. 2009; Feely et al. 2009; Ries 2011*a*; Byrne and Fitzer 2019). Ocean acidification (OA) is the result of carbonate undersaturation in seawater caused by increases in atmospheric carbon dioxide that are absorbed by seawater and form excess hydrogen and bicarbonate ions that inhibit the precipitation of carbonates. If carbonates are limited in seawater, calcifying organisms might have difficulty producing and maintaining their shells (Ries 2011*a*; Byrne and Fitzer 2019). Rapid increases in carbon dioxide and subsequent OA have been implicated in several major extinction events in the fossil record (Zachos et al. 2005; Kump et al. 2009; Kiessling and Simpson 2011; Greene et al. 2012; Honisch et al. 2012; Zeebe 2012; Clarkson et al. 2015; Henehan et al. 2019). OA is also a major consequence of our current carbon dioxide emissions, with some areas, such as the coast of California during upwelling season, already showing carbonate undersaturation (Chan et al. 2017), and experimental evidence showing negative consequences for many marine organisms (Kroeker et al. 2010, 2013; Byrne and Fitzer 2019). Organisms with carbonate skeletons are expected by be particularly vulnerable to OA because their skeletons are a primary means of defense against predators (Kroeker et al. 2014).

Potentially complicating matters, there are two carbonate polymorphs, calcite and aragonite, that are regularly used by marine organisms to create their skeletons, but have properties that make them differentially susceptible to both dissolution and predation. Calcite is more stable and resistant to dissolution (Ries 2011*a*), and is also cheaper for most organisms to produce (Palmer 1992). Aragonite is more susceptible to dissolution and energetically costly (Palmer 1992), but it is mechanically stronger than calcite, potentially providing greater resistance to durophagous predation. The conflicting trade-offs between calcite and aragonite may have important implications for the integrity of prey defenses, both in the future as a result of climate change, as well as in the fossil record.

Prey selection is also an obvious component of predation, as prey that are not frequently attacked will not experience the same selective pressures as those that are attacked more often. Particularly when observing repair scars in fossil systems, it may be difficult to interpret whether a difference in repair frequency between species is a result of predator preference, or differential success/failure rates between prey due to prey defenses (Leighton 2002; Alexander and Dietl 2003). In the case of crabs, some studies have shown them to select prey in a less than optimal manner, such as attacking smaller than expected prey (Juanes and Hartwick 1990; Juanes 1992), pursuing infaunal prey regardless of size or time spent (Smith et al. 1999; Dudas et al. 2005), and consuming entire clumps of mussels, including very small, non profitable individuals (Lin 1991). The ability of crabs to differentiate among and select for prey is therefore useful to help interpret repair scars in assemblages of their prey.

Repair scars, have been well studied in both the fossil record (Vermeij et al. 1980, 1981; Schindel et al. 1982; Vermeij 1983; Leighton 1999, 2002, 2011; Dietl and Kelley 2002; Alexander and Dietl 2003; Dietl et al. 2010; Richards and Leighton 2012; Dietl and Kosloski 2013; Mondal et al. 2014*a*; Stafford et al. 2015*b*; Mondal and Harries 2015; Pruden et al. 2018), and in modern ecosystems (Zipser and Vermeij 1978; Vermeij 1982*b*; Geller 1983; Alexander 1986; Schmidt 1989; Schindler et al. 1994; Cadée et al. 1997; Dietl and Alexander 1998, 2009; Alexander and Dietl 2001; Molinaro et al. 2014; Mondal et al. 2014*b*; Stafford et al. 2015*a*; Harper and Peck 2016; Tyler et al. 2019), with repair frequency typically used as a measure of comparison between samples. As mentioned, repair scars provide a record of unsuccessful, rather than successful attacks, so there can be some ambiguity in whether the frequency of scars was indicative of the number of attacks, or the success of predators. For example, if repair frequency increased between two samples, it could indicate that the number of attacks increased, but it could also mean that the predators were less successful and failed more often, resulting in the formation of more repair scars. To help differentiate between attack and success rates, as well as identify potential prey defenses or size refuges, the size at which attacks (repairs) occur may also be measured (Alexander and Dietl 2001; Leighton 2002; Richards and Leighton 2012; Mondal et al. 2014*b*; Pruden et al. 2018). If repair sizes decreased along with an increase in repair frequency, the most likely cause would be a decrease in predator success. If on the other hand, repair size did not change, repair frequency might be a reflection of attack rates. Increases in repair sizes associated with changes in carbonate saturation could also potentially indicate impaired prey defenses, and greater predator success.

In rocky intertidal communities along the west coast of North America, cancrid crabs, such as *Cancer productus* and *Romaleon antennarium*, are common and widespread generalist predators that feed on molluscs. The gastropods *Tegula* and *Nucella* are also abundant members of the same rocky shoreline communities, where they are commonly prey for crabs (Geller 1982*a*, 1983; Palmer 1985; Appleton and Palmer 1988; Marko and Palmer 1991; Bourdeau 2009, 2010*a*, 2011, 2012, 2013; Edgell 2010; Mach and Bourdeau 2011; Molinaro et al. 2014; Stafford et al. 2015*a*; Mendonca et al. 2017; Tyler et al. 2019). Not only are these species abundant, key members of their communities (e.g., Hull and Bourdeau 2017), but both crabs and gastropods have fossil records dating back at least to the Pleistocene (Menzies 1951; Valentine 1962; Nations 1975; Walker and Carlton 1995; Collins et al. 1996), and as such are an ideal model system for exploring predator-prey interactions through time. The goals of the project were to: 1) explore the effects of OA on the structural integrity of both gastropods, 2) identify patterns of crab prey selection, particularly between similar species, and 3) identify patterns of predation in repair scars across both spatial and temporal scales. By understanding how repair scar systems may manifest, potential consequences of human activity and climate change on predator-prey relationships can be identified.

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Chapter 2

Variation in the effects of ocean acidification on shell growth and strength in two intertidal gastropods[1]

2.1 Introduction

Ocean acidification (OA) from human-induced CO_2 emissions has negative effects on many marine organisms, leading to impaired physiological performance, modified species interactions, and potential ecosystem disturbances (Kroeker et al. 2014; Sanford et al. 2014*b*; Gaylord et al. 2015). For example, marine taxa that precipitate calcified shells, such as molluscs, may experience increased vulnerability to shell-crushing predation under OA (Orr et al. 2005; Hendriks et al. 2010; Gazeau et al. 2013). This trend could also be exacerbated by the fact that shell-crushing predators, such as crabs, appear to be less susceptible to seawater acidification (Amaral et al. 2012; Kroeker et al. 2013, 2014), although see Coffey et al. (2017). Increased costs of calcification therefore may have important implications for gastropods and other molluscs that use their shells to deter shell-crushing (durophagous) predation.

Durophagy has been a common method of predation since the Palaeozoic (Vermeij et al. 1981; Alexander and Dietl 2003; Leighton 2011). Molluscs, such as gastropods, are therefore dependent on their shells as an important defense against predation (Palmer 1979; Vermeij et al. 1981; Alexander and Dietl 2003). Mollusc shells have varying amounts of organic matrix, and, regardless of microstructural differences, have little ability to bend before catastrophic breakage/shattering occurs (Wainwright et al. 1976). Although such structures are therefore

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strong and rigid, they remain vulnerable to compressive and tensile forces exerted by shell-crushers. For example, durophagous crabs are capable of exerting large forces with their shell-crushing chelae (Taylor 2000). Additionally, crabs often apply methods of force-pulsing on mollusc shells, wherein the crab repeatedly point-loads the shell and creates material fatigue of the shell through propagation of microfractures, thereby increasing the likelihood of shell failure (Boulding and LaBarbera 1986). However, force-pulsing methods require predators to expend more time and energy (Boulding and LaBarbera 1986; Miller and LaBarbera 1995), and the existence of repair scars on shells documents the occurrence of unsuccessful attacks (Molinaro et al. 2014; Stafford et al. 2015*a*).

Complicating efforts to understand predator-prey interactions involving molluscs is the issue that molluscs demonstrate a variety of plastic responses that may increase the search time, and/or force, time, and energy that a durophagous predator must spend handling the shell (Kroeker et al. 2014). Morphological changes to the shell generally enhance resistance to predation (Zipser and Vermeij 1978), but often require additional shell calcification. For example, gastropods may increase shell ornamentation or thickness under threat of predation (Appleton and Palmer 1988; Avery and Etter 2006). Some gastropods are also capable of making changes to their general morphology that increases their shell strength (Bourdeau 2012), which could be critical if calcium carbonate becomes limited.

In addition, behavioural changes from exposure to predation cues may cause animals to attenuate their foraging activities and can thereby reduce growth (Appleton and Palmer 1988; Chivers and Smith 1998; Trussell et al. 2003). Because smaller molluscan shells are typically weaker (Currey and Hughes 1982), they are more vulnerable to shell-crushing predation. Organisms exposed to both OA and predation might therefore experience reduced growth that would make them critically vulnerable to predation. However, seawater acidification is known to disrupt antipredatory fleeing responses to sea stars in some gastropods (Jellison et al. 2016). The potentially mixed effects of both OA and predation risk on both gastropod shell growth, and plastic shell responses, are therefore poorly understood, as there has been only one other long-term study wherein gastropods were exposed to both OA and predator cues (Landes and Zimmer 2012).

Responses to ocean acidification, such as changes to shell integrity, may be relatively inconspicuous, yet important. In the case of shelled gastropods, for instance, experiments that quantify OA effects on behaviour, shell growth, or shell thickness (Landes and Zimmer 2012; Kroeker et al. 2014; Jellison et al. 2016) provide valuable information about predation risk. However, these studies may also remain incomplete, as size is not the only metric or shell property by which prey resist durophagy. Shell strength, while less conspicuous and more difficult to measure, provides a more accurate metric as it can be used to assess resistance to shell crushing directly. Thus, although researchers often assume stasis in the susceptibility to predation of species when shell growth appears resilient to OA (Gazeau et al. 2013; Kroeker et al. 2013; Lord et al. 2017), shell strength could also be affected. For example, some species of gastropod exposed to acidification exhibit no change in growth, yet experience increased shell dissolution (Nienhuis et al. 2010), which would presumably have a negative effect on shell strength. Most biomechanical studies that examine the impacts of OA on shell strength are limited to bivalves (Welladsen et al. 2010; Gaylord et al. 2011; Fitzer et al. 2015), with few including gastropods (Amaral et al. 2012; Coleman et al. 2014; Leung et al. 2017*b*), indicating that there is strong value in conducting further tests of shell strength in a broader array of calcifying taxa, such as gastropods, which are abundant and diverse constituents of coastal food webs.

Although considerable effort in OA research has aimed to identify common patterns across taxa and environments (Gazeau et al. 2013; Kroeker et al. 2014; Gaylord et al. 2015), species-level variation can be equally relevant to understanding the ecological consequences of acidification (Sanford et al. 2014*b*). For example, in rocky intertidal habitats along the northeastern Pacific, the gastropods *Tegula funebralis* (Trochoidea) and *Nucella ostrina* (Muricoidea) are common prey for shell crushing predators such as crabs. However, the two gastropods have different shell microstructure and composition, responses to predation, life histories, and ecological roles. *T. funebralis*, a grazer, has a nacreous (columnar aragonite plates/crystals) shell and periostracum (Geller 1982*a*), while *N. ostrina*, a barnacle and mussel drill, has an outer homogenous calcite layer and inner cross-lamellar aragonite layer with no periostracum (Watabe 1988; Avery and Etter 2006). While calcite is more resistant to dissolution, nacre is mechanically stronger than both calcite and other forms of aragonite (Watabe 1988). Behaviourally, when exposed to predation cues, both species flee the water (Jacobsen and Stabell 2004; Mach and Bourdeau 2011), but several species of *Nucella*, including *N. ostrina*, also respond to predation cues morphologically in the form of shell thickening/inducible defenses (Appleton and Palmer 1988; Pearson 2004), as well as changes in shape (Bourdeau 2012). However, past studies have indicated that there may not be a true induced defense in *N. ostrina*, and instead, the species may simply reduce its growth when exposed to predation cues (Bourdeau 2011). One could therefore imagine a scenario where the two species display different growth or calcification responses to OA that would make one species comparatively more or less vulnerable to durophagous predation. Any changes to the vulnerability of one species over the other under seawater acidification could potentially lead to changes in their favourability to predators, shifts in the rankings of prey by predators, and alterations to the strengths of associated trophic links in food webs (Kroeker et al. 2014).

Here, we address such issues of variability among species and the potential for overlooked responses, such as shell strength, in gastropods by exposing two species of intertidal gastropods from the west coast of North America to both seawater acidification (decreased pH of ~0.5 units) and predation cue for six months. We measure both shell growth and strength as proxies for resistance to durophagy, and consider the implications of the responses that these two species exhibit.

2.2 Materials and Methods

2.2.1 Specimens

To explore the potential ecological implications of OA on gastropods threatened by durophagous predation, juveniles (small individuals) of both *Tegula funebralis* and *Nucella ostrina* were collected from the northern side of Horseshoe Cove in the Bodega Marine Reserve (BMR) near Bodega Bay, California (38°19'0"N 123°04'14"W) in November and December of 2016 in accordance with BMR regulations. Collected gastropods were acclimated to laboratory conditions at Bodega Marine Laboratory for at least three weeks. Initial shell height and width of each gastropod was measured using digital calipers (height and width of *T. funebralis* and *N. ostrina*, respectively: 6.14 ± mm 0.70, 7.77 mm ± 0.81; 12.06 mm ± 1.43, 7.95 mm ± 0.98), and 160 individuals of each species most similar in size were selected for subsequent experiments.

2.2.2 Methods

To compare the effects of both OA and predation cues on shell growth, the experiment was divided into four water treatments: 1) ambient water, no conspecific cue; 2) ambient water, injured conspecific cue present; 3) low pH water, no conspecific cue; 4) low pH water, injured conspecific cue present. Gastropods were divided randomly into 32 groups of 10 individuals (16 groups per species). Each group was randomly assigned to a 10L tanks (n = 2 species x 4 treatments x 4 replicate tanks per treatment = 32 tanks total. The growing edge of each gastropod shell was marked with a thin line of coloured nail polish, which provided individuals with unique identifying tags and allowed easy determination of growth during the experiment.

Water conditions for each of the four treatments were controlled, monitored, tested, and reset every 24 hours for 185 days. Once a day, each tank was filled with 7L of water from one of four source (sump) tanks: 2 replicate ambient tanks, and 2 replicate low pH tanks. This volume was sufficient to maintain animal health and minimize shifts in seawater chemistry due to respiration. Water was acquired from the laboratory seawater supply, and was dual filtered to 30 then 5 microns. The "low pH" water treatments were created daily through direct chemical manipulation via an equimolar addition of 1 M hydrochloric acid (HCl) and 1 M sodium bicarbonate ($NaHCO_3$) (Jellison et al. 2016) which increased dissolved inorganic carbon (DIC) while maintaining alkalinity and reproduced the chemical changes caused by the addition of CO_2, as specified by international standards (Riebesell et al. 2010). Water for the "ambient" treatments was left unchanged to reflect the natural daily and seasonal changes experienced by organisms around Bodega Bay, including a period of upwelling with naturally lower water pH in the spring months. "Low pH" conditions approximated a drop of 0.5 pH units (pH_{total}), as determined using the software CO2Calc (Robbins et al. 2010). Each of the 32 tanks was placed in a flow-through seawater table which acted as a temperature bath (mean ± SD, 12.26°C ±1.00). TidbiT® temperature loggers, which recorded temperature every 15 minutes, were placed in tanks on opposite corners of the seawater table to confirm temperature did not differ across the table and that any spatial segregation between pH or cue treatments would have minimal effects on the results. After each experimental tank was filled with the appropriate water each day, an airtight lid was placed on the tanks to prevent off-gassing of the low-pH treatments. There was enough headspace for the gastropods to leave the water, allowing for the possibility of an anti-predatory "fleeing" response for those exposed to the injured conspecific cue. An airline was placed at the bottom of each tank (< 1 bubble/second) to provide water circulation and prevent a temperature or pH cline from developing. In these respects, each tank imitated a tide pool, a common environment for both species (Jellison et al. 2016).

To examine the effects of predation threats, treatments also included a "no cue" control, as well as a "cue" condition in which an injured conspecific was used to signal the threat of predation, as both species are known to respond to injured conspecific cues (Jacobsen and Stabell 2004; Mach and Bourdeau 2011). An extra individual of each species was crushed using a pair of pliers, and the dead gastropod was then mixed with 100 mL of seawater and left for 5 to 10 minutes. Crushing a conspecific was used as a proxy for the chemical effluent simulated by crab crushing predation, as other methods of predation (e.g., being consumed by a sea star) do not usually result in a shell being crushing. While a combined crab and crushed conspecific cue might elicit a stronger response (Appleton and Palmer 1988), the use of a crushed conspecific cue alone was used as a more conservative, generalized fear response that would be generated by crushing predation, regardless of the predator's identity (e.g., *Cancer productus* or *Romaelon antennarium*) or diet (e.g., Scherer & Smee 2016). 10 mL of the "dead snail" effluent water was then pipetted into each of the appropriate tanks. This cue was added three times a week to appropriate tanks.

The gastropods were given sufficient food to prevent competition among individuals. *T. funebralis* were fed small pieces of the macroalgae *Pelvetiopsis limitata*, *Mastocarpus papillatus*, and *Ulva lactuca*. *N. ostrina* were fed barnacles (*Balanus glandula* and *Chthamalus dalli*) attached to small rocks that were cleaned of all other organisms and any adherent sediment or debris. Food was refreshed as needed (usually once per week) and to avoid any additional effects of pH on the food source.

To ensure tight control of water conditions - temperature, dissolved oxygen, salinity, and pH (mV) - of the 4 sumps were recorded each day using a YSI ProPlus sensor, that was in turn calibrated against spectrophotometric pH measurements made on the total scale. Temperature data from the YSI were comparable to the TidbiT® data. Daily bottle samples were taken from each sump for analysis of total alkalinity using a Metrohm 855 Robotic Titrosampler to ensure that the addition of HCl and $NaHCO_3$ had not changed the alkalinity. An additional water sample was pulled weekly from each sump and pH was determined using an Ocean Optics Jaz Spectrometer. Spectrometer pH and alkalinity data were run through CO2Calc to determine the *in situ* pH and pCO_2.

After six months (180 and 185 days for *N. ostrina* and *T. funebralis*, respectively), a final set of height and width measurements were taken for each gastropod individual to determine differences in growth between each treatment over the course of the six months. Specimens were then prepared for the second experiment to measure any differences in shell strength between the four treatments. The gastropods were euthanized by placing them in a freezer (-18°C). After 24 hours, the gastropods were then thawed and the body tissue was carefully removed using small forceps. Shells were air dried for several weeks prior to biomechanical tests. In certain species, material properties of dried shells can differ modestly from those of wet shells; however, the focus of the current experiment was on relative changes across size and species as a function of pH treatment. Freezing is a common, humane method of euthanasia not known to affect shell structure (A. R. Palmer, pers. comm) and is comparable to other studies of shell strength in gastropods (Coleman et al. 2014).

A primary goal of measuring shell strength was to determine whether OA might weaken shells sufficiently to be crushed outright by crabs. After weighing each shell using a scale to 0.0001 g accuracy, 20 specimens were randomly selected from each of the 4 treatments for use in biomechanical tests. Dental plaster was poured into 1 cm tall x 2.5 cm wide cups and the gastropods were partially embedded in the plaster as it dried (Fig. 2.1). Shells were aligned with the axis of coiling perpendicular to the dental plaster, and the apertural lip facing vertically towards the upper plate of an Instron® universal testing system (Fig. 2.1), similar to another OA study (Coleman et al. 2014). The shell orientation ensured that experimental growth would be the primary source of contact with the Instron®, and roughly simulated the orientation in which a crab would first pick up a gastropod to attempt a static crush (Zipser and Vermeij 1978).

Each shell was crushed to total failure (any fracturing of the shell above the body whorl, indicating the gastropod would be unable to survive the crush). Shells of both species broke in a consistent manner (a distinct “popping” or “blow out” of the spire and/or apex). The force to induce total failure of the shell was recorded (maximum compression load, N). After initial analyses, p-values for *N. ostrina* tests were nearly significant ($p = 0.06$), so an additional 10 *N. ostrina* from each treatment were crushed to ensure sample size was not limiting statistical power.

2.2.3 Analyses

To determine the effects of both pH and predation cues on shell growth, generalized linear mixed models (GLMM) (with sumps and tanks as random effects, and pH and predation cue as fixed effects) were used. Separate tests were run for both height and width of each species using the change in size measured from the beginning and the end of the experiment as the measure of growth. For each set of growth measurements, four GLMMs were fit (all had sumps and tanks as random effects): a null model with only random effects; a pH-only model, a cue-only model, and a full mixed model with both pH and cue as fixed effects. For *T. funebralis,* Gamma distributions with a log link function were used given that the data were skewed to zero as many *T. funebralis* specimens did not grow (skew > 1). To accommodate the Gamma distribution, which does not handle zero data, half of the smallest growth increments were added to all zero data (0.005 mm), which is a common data transformation for addressing this problem (Berry 1987). For *N. ostrina*, a Gaussian distribution was used, as the data were roughly normally distributed (Shapiro-Wilk test for normality, $p > 0.05$). The best fit model for each growth series was determined as the model with the lowest Akaike information criterion (AIC). Models were ranked from best to worst (1 – 4). Log-likelihood ratio tests were conducted to determine which models were statistically distinguishable from the null and from each other. All GLMM models and log-likelihood ratio tests were conducted using the lme4 package in R (version 3.4.4), and the models were plotted and checked using the DHARMa package.

Shell strength (maximum force recorded at the point of shell failure) was analyzed using two-way ANCOVAs to determine the effects of pH and cue on shell strength, with dry shell mass as a covariate of the response variable (maximum crushing force). A Shapiro-Wilk test for normality and a Levene’s test for homogeneity of variances were also conducted to confirm the data met the model assumptions. To test whether any spatial segregation of treatments or tanks influenced our results, additional two-way ANCOVAs were run on tank averages. All ANCOVA analyses were conducted using the XLSTAT program for Microsoft Excel.

Due to logistical constraints concerning tank access, the cue treatments for both species were positioned on one side of the seawater table. The spatial segregation of cue/no-cue treatments caused certain aspects of the experiment to be pseudoreplicated (side of the water table confounded with cue treatment). While we acknowledge this segregation may cause challenges for completely unambiguous interpretation of the results, it is important to note that in all other respects, experimental conditions were carefully controlled, leading to no obvious differences between the two sides of the table (the table was only about 60 cm wide, and tanks were placed less than 5 cm apart). For example, the temperature loggers placed in tanks on opposite corners of the sea table (including a cue and no-cue tank) were indistinguishable, and seawater flow was perpendicular to the placement of all tanks.

2.3 Results

2.3.1 Shell Growth

Shell growth of *Tegula funebralis* decreased significantly under low-pH conditions and in the presence of predation cues, with log-likelihood ratio tests indicating that a full mixed effects model including pH, cue, and their interaction as fixed effects significantly outperformed all other models (Log-likelihood test, $p < 0.0001$) (Table 2.1, Figs. 2.2B, C, D, I, J, 2.3A, 2.4A). In particular, *T. funebralis* reared under low pH grew 83% less than when in ambient treatments (Log-likelihood test, width $p = 0.001$) (Tables 2.1, 2.2), with 17 individuals raised under low pH not growing at all (Figs. 2.3A, 2.4A), and most experiencing dissolution resulting in pitting and small holes around the apex (Fig. 2.2C, D, I, J). Injured conspecific cues also had a significant effect on shell growth as *T. funebralis* exposed to cue grew 63% less than those not exposed to cue (Log-likelihood test, width $p = 0.0085$) (Tables 2.1, 2.2, Figs. 2.2B, D, 2.3A, 2.4A).There is likely a significant interaction between pH and cue, possibly due to a zero-boundary effect, as pH reduced growth such that cue could not decrease growth additively in mixed treatments (there could not be growth less than zero) (Figs. 2.3A, 2.4A).

In contrast, shell growth in *Nucella ostrina* was not affected by pH, as pH models were indistinguishable from the null (Log-likelihood test, width $p = 0.6008$)) (Table 2.1, Figs. 2.2G, H, 3B, 4B). Instead, both cue models (height and width) performed the best, indicating that only the injured conspecific cue significantly affected growth in *N. ostrina* (Log-likelihood tests, $p < 0.0001$), with cue-exposed specimens growing 34% less than those not exposed to cue (Table 2.1, Figs. 2.2F, H, 2.3B, 2.4B), consistent with previous reports (Bourdeau 2011; Lord et al. 2017). Similar to Bourdeau (2011), there was no evidence of shell thickening (mass to size ratios between treatments were indistinguishable) (Table 2.2) or changes to morphology (Fig. 2.4) indicative of an induced defense, despite inducible defenses often being observed for the genus (Appleton and Palmer 1988; Pearson 2004; Bourdeau 2011, 2012).

Note that for all models for both species, the defined random effects, sumps and tanks, had standard deviations close to zero (all < 1), indicating that these random effects had no appreciable effect on growth. As the residual error is also generally low, the results are not likely a function of any potential artifacts due to tank or treatment placement, and most of the explanatory power for changes in growth can be safely attributed to the differences between treatments.

For cue treatments, when exposed to cue effluent, both species left the water within ~10 minutes. Individuals often hid, clustered, or remained above the water even after 24 hours. While it was not possible to measure how often gastropods returned to the water, casual observation throughout the experiment suggests that gastropods exposed to cue spent less time in the water. Lack of induced shell thickening or changes in morphology (Fig. 2.4) indicates that similar to *T. funebralis*, cue exposed specimens of *N. ostrina* simply grew less.

2.3.2 Shell Strength

While the two species demonstrated very disparate results in terms of growth, with *T. funebralis* shell growth strongly impacted by pH, but *N. ostrina* being unaffected, biomechanical tests indicated both species experienced reduced shell strength when exposed to pH (Table 2.3). However, the effect size was different, and *T. funebralis* experienced much greater reductions in shell strength from exposure to low pH than did *N. ostrina*. *T. funebralis* shells exposed to low pH were significantly (41%) weaker than ambient shells, regardless of size, failing at forces ~171 N less than those grown under ambient conditions (Two-way ANCOVA, $F_{72,1} = 18.049$, $p < 0.0001$) (Table 2.3, Fig. 2.5A). Shell strength in *N. ostrina* was compromised by pH, despite resilient growth, with shells exposed to low pH being 9% weaker and failing at forces ~44 N less than ambient shells (Two-way ANCOVA, $F_{112,1} = 6.591$, $p = 0.0116$) (Fig. 2.5B). This pattern also held when average values for each tank were used in the analyses (Two-way ANCOVA, $F_{8,1} = 7.119$, $p = 0.0280$ (*T. funebralis*) and $F_{8,1} = 5.932$, $p = 0.0410$ (*N. ostrina*)) (Table 2.3).

For both species, shell strength was significantly correlated with size (mass) ($r = 0.4140$, Two-way ANCOVA, $F_{72,1} = 20.670$, $p < 0.0001$ [*T. funebralis*], $r = 0.460$, Two-way ANCOVA, $F_{112,1} = 87.949$, $p < 0.0001$ [*N. ostrina*]), with larger shells requiring more force to crush to total failure (breakage of the spire) (Table 2.3, Fig. 2.5). However, it is critical to reiterate that shells exposed to low-pH failed at lower forces than did shells of the same size grown under ambient-pH conditions (Fig. 2.5). Conspecific cues did not affect shell strength in either species, indicating cue simply reduced growth for both species (Table 2.3).

2.4 Discussion

Reductions in shell growth and/or strength suggest increased vulnerability of both gastropod species to predation under OA. Independent of growth, shells of both *Tegula funebralis* and *Nucella ostrina* grown under low pH conditions are “cryptically” vulnerable in that low pH shells are weaker than ambient pH shells of the same size (Fig. 2.5). A study that only examined shell growth might have concluded that *N. ostrina* is unaffected by OA, yet we demonstrate OA reduced shell strength. Our results therefore indicate that measures of shell strength are critical to assessing the vulnerability of calcifiers to OA properly. For example, a gastropod that may be of a size sufficient to avoid shell-crushing predation under ambient conditions may be vulnerable at low pH conditions, such as those predicted for the end of the 21st century (Orr et al. 2005).

Decreased shell growth under OA further compounds the effects of shells weakened by exposure to OA, making it more difficult for gastropods to grow to a size which would allow them to avoid shell-crushing predation, resulting in smaller individuals that are critically vulnerable to predators such as crabs. In addition, the presence of predators also reduces shell growth, as fearful gastropods spend less time foraging (Trussell et al. 2003), further compromising shell growth under future OA conditions. For example, mollusc shells typically require more force to fail than can be exerted by their predators (Boulding and LaBarbera 1986; Miller and LaBarbera 1995), yet 14 (of 40) of the *T. funebralis* grown under low pH and/or cue conditions failed at forces less than can be produced by predators such as *Cancer productus* (140 - 264 N) (Taylor 2000) (Fig. 2.5A). Thus, OA could produce conditions where crabs could crush *T. funebralis* outright, instead of the usual force-pulsing or peeling methods which are more time consuming and have less guarantee of success (Zipser and Vermeij 1978). For instance, *C. productus* in the field take more than 9 minutes on average to peel an individual *T. funebralis* (L.R., Leighton, unpublished data). *T. funebralis* takes significantly more time to grapple and handle, with lower rates of success (over 7 minutes, 61% success) than those for *N. ostrina* (2 minutes, 96% success), which can be crushed, rather than peeled (Mendonca et al. 2017). In contrast, a typical static crush can take less than a minute (Mendonca et al. 2017). The combined effects of reduced shell strength and growth may therefore result in significantly decreased handling times for durophagous predators (Leighton 2002), creating indirect ecological consequences wherein the per capita consumption rates of crabs on gastropods may increase (Kroeker et al. 2014).

Impaired strength and growth may also increase the vulnerability of gastropods by increasing the time required to reach a size refuge wherein resistance to durophagy is more likely. In particular, *T. funebralis* is a slow growing species (Frank 1975). Over the course of the six-month experiment, there were 4 (of 80) *T. funebralis* from the ambient treatments which did not grow, yet there were 17 (of 80) from low pH treatments that did not grow. Decreased growth rates, coupled with impaired shell strength, therefore suggest that species such as *T. funebralis* may spend considerably more time in a critically vulnerable state. These effects would be even more pronounced in environments where gastropods experience greater predation risks.

In addition, many of the *T. funebralis* exposed to low pH developed small, complete holes through the shell near the apex (Fig. 2.2C, D, I, J). While apex abrasion is typical for *T.*

funebralis (Geller 1982*a*), it rarely produces overt holes, especially in juveniles. Holes present substantial weakness to shell crushing predators, and may make affected individuals more detectable to chemosensitive predators (octopods, crabs, sea stars) even if the gastropod foot is retracted, suggesting strong ecological consequences for *T. funebralis* due to OA. Overall, the consequences of seawater acidification appear to be far more severe for *T. funebralis* than for *N. ostrina*.

The dissimilar effects of OA on two gastropods that co-exist in many of the same habitats signals the extensive implications of OA for coastal ecosystems. For instance, as *T. funebralis* experienced both reduced growth and shell integrity to a far greater extent than *N. ostrina*, it is conceivable that the per capita consumption rate of crabs feeding on *T. funebralis* populations might increase relative to *N. ostrina*, especially if the weakened *T. funebralis* become a more favoured prey item. Furthermore, *T. funebralis* shells are proportionately stronger than shells of *N. ostrina* (based on both mass and size). As *T. funebralis* only exhibit behavioural fleeing responses to predation cues (Jacobsen and Stabell 2004), *T. funebralis* appears to rely on its shell and ability to flee to deter predation. Not only are crabs much more mobile than gastropods, but *T. funebralis* also exhibit impaired antipredatory responses under decreased seawater pH (Jellison et al. 2016). Therefore, the large reductions in shell growth and strength, combined with impaired antipredatory responses, indicate that *T. funebralis* are likely to be increasingly vulnerable to predation under seawater acidification. Disproportionate effects on any one species in a food web could therefore not only have notable consequences for populations of species, such as *T. funebralis*, but could also potentially change the ranking or favourability of prey items, increasing predation pressure on those species.

Shell composition also may contribute to the different responses to OA for the two gastropods. While nacre (produced by *T. funebralis*) is mechanically stronger than other shell forms, it is energetically expensive to produce and susceptible to dissolution (Currey 1988). In contrast, calcite (the outer layer of *N. ostrina* and other muricoid shells) is energetically cheaper and more resistant to dissolution (Currey 1988; Palmer 1992), possibly buffering the effects of OA (Nienhuis et al. 2010). Examining shell composition and strength therefore provides insight into how OA affects shells, and which species may be more or less vulnerable to OA. Taxonomic groups of molluscs have predictable shell compositions (Watabe 1988), yet composition as a means of identifying susceptibility to OA has been underutilized (Leung et al. 2017*a*).

While it is possible that crabs may also be affected by OA (Landes and Zimmer 2012; Dodd et al. 2015; Coffey et al. 2017; Lord et al. 2017), the literature is less conclusive for crabs, other crustaceans, and arthropods in general (Amaral et al. 2012; Kroeker et al. 2013, 2014), minimally suggesting asymmetrical effects on molluscs relative to their crustacean predators. Although one study has shown mechanical weakness of crab chelae material (Coffey et al. 2017), material weakness of the chelae may not affect the muscular strength of the chelae or ability of the crab to force-pulse, as the forces exerted by crabs are still typically much less than that which is required to break the shells of their prey outright (Boulding and LaBarbera 1986; Miller and LaBarbera 1995). Another long term study found that the length of the claw closer musculature of green crabs, *Carcinus maenas*, decreased with exposure to OA, yet claw strength appeared unaffected by OA and was instead significantly stronger with increased temperature (Landes and Zimmer 2012).

The cryptic reductions in shell strength, regardless of size, suggest easily overlooked consequences of OA that will increase the vulnerability of calcifying organisms to predation, and emphasize the importance of biomechanical experiments. Direct tests of shell strength are therefore critical to evaluate fully the vulnerability of calcifying organisms to OA. Impaired shell strength and growth of gastropods also suggest indirect ecological effects, potentially reducing handling times for prey and increasing the per capita consumption rates on gastropod populations. However, the dissimilar effects of OA on both species also suggests that shifts in biotic interactions will be asymmetrical, further disrupting the balance of these ecosystems, and highlighting the importance of species-level assessments. We are therefore likely underestimating the ecological effects of OA, particularly the differential increased vulnerability of calcifiers to predation.

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Table 2.1

Summary information for growth GLMMs and log-likelihood comparisons of models used to determine the effects of pH and cue on shell growth.

Models were ranked (1 – 4) based on Akaike information criterion (AIC) scores (lower AIC scores were considered better models). Each model was then compared using log-likelihood tests to determine which models statistically outperformed others.

Mixed Model Info (Tank and Sump as random effects)											
	AIC	**BIC**	**logLik**	**deviance**	**df.resid**		**AIC**	**BIC**	**logLik**	**deviance**	**df.resid**
***T. funebralis* Height**						***N. ostrina* Height**					
pH*Cue	-92.2	-70.7	53.1	-106.2	153	Cue only	621.4	636.8	-305.7	611.4	155
pH only	-87.5	-72.2	48.8	-97.5	155	pH*Cue	625.1	646.6	-305.5	611.1	153
Cue only	-75.2	-59.8	42.6	-85.2	155	Null (random effects only)	635.4	647.7	-313.7	627.4	156
Null (random effects only)	-73.9	-61.6	40.9	-81.9	156	pH only	637.1	652.4	-313.5	627.1	155
***T. funebralis* Width**						***N. ostrina* Width**					
pH*Cue	-69.6	-48.0	41.8	-83.6	153	Cue only	502.4	517.7	-246.2	492.4	155
pH only	-54.8	-39.4	32.4	-64.8	155	pH*Cue	505.7	527.3	-245.9	491.7	153
Cue only	-50.8	-35.4	30.4	-60.8	155	Null (random effects only)	520	532.3	-256	512	156
Null (random effects only)	-45.9	-33.6	26.9	-53.9	156	pH only	521.8	537.1	-255.9	511.8	155

Model comparisons - log likelihood tests = Pr (> Chisq) Model Ranks (1, best - 4, worst)											
***T. funebralis* Height**						***N. ostrina* Height**					
		4	1	2	3			3	2	4	1
		Null	pH*Cue	pH only	Cue only			Null	pH*Cue	pH only	Cue only
4	Null					3	Null				
1	pH*Cue	**< 0.0001**				2	pH*Cue	**0.0010**			
2	pH only	**< 0.0001**	**0.0131**			4	pH only	0.5736	**0.0003**		
3	Cue only	0.0698	**< 0.0001**	1.0000		1	Cue only	**< 0.0001**	0.8443	**< 0.0001**	
***T. funebralis* Width**						***N. ostrina* Width**					
		4	1	2	3			3	2	4	1
		Null	pH*Cue	pH only	Cue only			Null	pH*Cue	pH only	Cue only
4	Null					3	Null				
1	pH*Cue	**< 0.0001**				2	pH*Cue	**0.0001**			
2	pH only	**0.0010**	**< 0.0001**			4	pH only	0.6008	**< 0.0001**		
3	Cue only	**0.0085**	**< 0.0001**	1.0000		1	Cue only	**< 0.0001**	0.7255	**< 0.0001**	

Table 2.2

Summary data for each treatment and analyses of shell growth and strength. Average growth and strength measurements (± standard deviation) are presented for each treatment. Tank averages are also included for use in strength analyses (Max Load and Mass).

Summary Data (Mean ± SD)											
		Growth		**Strength**				**Growth**		**Strength**	
Tegula funebralis						***Nucella ostrina***					
Treatments											
		Height (mm)	**Width (mm)**	**Mass (g)**	**Max Load (N)**			**Height (mm)**	**Width (mm)**	**Mass (g)**	**Max Load (N)**
Ambient No Cue		0.82 ± 0.40	1.21 ± 0.54	0.2001 ± 0.0612	453.0956 ± 104.6257	Ambient No Cue		4.66 ± 1.72	3.46 ± 1.20	0.5997 ± 0.1787	499.7232 ± 109.4207
Ambient Cue		0.38 ± 0.29	0.39 ± 0.32	0.1632 ± 0.0483	383.3014 ± 118.0891	Ambient Cue		2.97 ± 1.50	2.17 ± 1.10	0.5570 ± 0.2070	500.2285 ± 134.4334
Low pH No Cue		0.12 ± 0.16	0.12 ± 0.18	0.1351 ± 0.0395	261.8708 ± 109.0351	Low pH No Cue		4.96 ± 1.86	3.56 ± 1.20	0.6372 ± 0.2265	470.1941 ± 149.4745
Low pH Cue		0.14 ± 0.15	0.14 ± 0.18	0.1282 ± 0.0383	231.7610 ± 112.9203	Low pH Cue		3.35 ± 1.74	2.46 ± 1.13	0.5022 ± 0.1459	441.7045 ± 96.8122
Tank Averages											
Ambient No Cue	1	0.86 ± 0.37	1.53 ± 0.35	0.1915 ± 0.0553	390.1840 ± 75.3266	Ambient No Cue	1	4.14 ± 1.95	3.58 ± 1.36	0.6034 ± 0.1193	536.3550 ± 64.2289
	2	0.90 ± 0.36	1.59 ± 0.37	0.2312 ± 0.0658	544.0999 ± 114.6645		2	4.68 ± 1.54	3.72 ± 1.17	0.6988 ± 0.0896	530.5209 111.3520
	3	0.59 ± 0.35	0.80 ± 0.56	0.1570 ± 0.0244	419.9323 ± 96.7382		3	4.10 ± 1.64	2.94 ± 1.21	0.4782 ± 0.2257	455.1054 ± 136.1470
	4	0.95 ± 0.46	0.91 ± 0.35	0.2207 ± 0.0754	485.1661 ± 84.3162		4	5.72 ± 1.44	3.61 ± 1.06	0.6158 ± 0.1887	475.1841 ± 107.5128
Ambient Cue	5	0.58 ± 0.32	0.48 ± 0.36	0.1567 ± 0.0533	333.8214 ± 105.1325	Ambient Cue	5	2.25 ± 1.10	1.86 ± 0.87	0.4123 ± 0.1115	395.9556 ± 49.3997
	6	0.40 ± 0.26	0.33 ± 0.33	0.1326 ± 0.0278	295.3121 ± 62.6638		6	3.48 ± 1.36	2.58 ± 1.12	0.6753 ± 0.1283	558.2881 ± 93.2567
	7	0.33 ± 0.24	0.28 ± 0.33	0.2120 ± 0.0547	447.5098 ± 150.0790		7	3.20 ± 2.03	2.21 ± 1.47	0.5577 ± 0.3343	484.7601 ± 189.1868
	8	0.23 ± 0.25	0.35 ± 0.30	0.1514 ± 0.0099	456.5624 ± 64.3060		8	2.95 ± 1.30	2.02 ± 0.88	0.5646 ± 0.1151	546.9424 ± 113.4248
Low pH No Cue	9	0.08 ± 0.14	0.18 ± 0.25	0.1332 ± 0.0306	229.6169 ± 60.8161	Low pH No Cue	9	5.84 ± 1.10	4.17 ± 0.79	0.8196 ± 0.0616	527.0612 ± 82.3096
	10	0.14 ± 0.17	0.15 ± 0.16	0.1479 ± 0.0510	333.4010 ± 125.8354		10	5.36 ± 1.89	3.62 ± 1.20	0.5893 ± 0.2175	469.3560 ± 150.6728
	11	0.15 ± 0.15	0.08 ± 0.16	0.1507 ± 0.0447	268.0427 ± 118.3908		11	4.62 ± 2.54	3.43 ± 1.71	0.6137 ± 0.2913	496.2755 ± 184.5453
	12	0.10 ± 0.18	0.09 ± 0.15	0.1023 ± 0.0087	213.1243 ± 124.4557		12	4.01 ± 1.25	3.01 ± 0.71	0.5363 ± 0.1157	384.4776 ± 110.8281
Low pH Cue	13	0.13 ± 0.11	0.18 ± 0.20	0.1152 ± 0.0320	294.3102 ± 162. 5259	Low pH Cue	13	3.71 ± 1.12	2.63 ± 0.82	0.5613 ± 0.0842	483.0997 ± 93.2443
	14	0.15 ± 0.19	0.16 ± 0.11	0.1514 ± 0.0606	188.9664 ± 123.1121		14	5.00 ± 1.70	3.50 ± 1.27	0.6101 ± 0.1697	477.1739 ± 107.9593
	15	0.16 ± 0.19	0.11 ± 0.16	0.1254 ± 0.0116	233.5166 ± 103.7632		15	2.68 ± 1.44	1.97 ± 0.83	0.4295 ± 0.1171	400.7871 ± 95.3104
	16	0.11 ± 0.10	0.11 ± 0.22	0.1209 ± 0.0345	210.2509 ± 21.6145		16	2.02 ± 1.10	1.75 ± 0.70	0.4122 ± 0.1086	405.0764 ± 64.0759

Table 2.3

Two-way ANCOVA results of pH and cue treatments on shell strength. Maximum force (N) was used as the response variable for shell strength, and shell mass (g) was the covariable, used as a proxy for size. An additional set of ANCOVAs was run on average strength (N) and size (g) measurements for each tank.

Strength Two-Way ANCOVA (Strength (N), with mass (g) as covariate)											
Tegula funebralis						***Nucella ostrina***					
(based on strength of individual shells)											
	Sum of squares	**Df**	**Mean square**	**F**	**P**		**Sum of squares**	**Df**	**Mean square**	**F**	**p**
pH	179045.405	1	179045.450	18.049	**<0.0001**	pH	54230.240	1	54230.240	6.591	**0.0116**
Cue	7604.150	1	7604.150	0.767	0.3842	Cue	18463.120	1	18463.120	2.244	0.1370
Mass	205056.650	1	205056.650	20.670	**<0.0001**	Mass	723664.730	1	723664.730	87.949	**<0.0001**
pH*Cue	172.400	1	172.400	0.017	0.8955	pH*Cue	2096.570	1	2096.570	0.255	0.6147
pH*Mass	4698.520	1	4698.520	0.474	0.4935	pH*Mass	4965.300	1	4965.300	0.603	0.4389
Cue*Mass	458.350	1	458.350	0.046	0.8304	Cue*Mass	8.670	1	8.670	0.001	0.9740
pH*Cue*Mass	1139.440	1	1139.440	0.115	0.7357	pH*Cue*Mass	8013.290	1	8013.290	0.974	0.3258
Within	714253.900	72	9920.000			Within	921564.300	112	8228.000		
Total	1586311.100	79				Total	1861381.900	119			
(based on average shell strength per tank)											
	Sum of squares	**Df**	**Mean square**	**F**	**P**		**Sum of squares**	**Df**	**Mean square**	**F**	**p**
pH	21538.204	1	21538.204	7.119	**0.0280**	pH	6655.959	1	6655.959	5.932	**0.0410**
Cue	1851.492	1	1851.492	0.612	0.4570	Cue	2119.721	1	2119.721	1.889	0.2070
Mass	119980.392	1	119980.392	38.658	**<0.0001**	Mass	27822.261	1	27822.261	24.797	**0.0010**
pH*Cue	1385.911	1	1385.911	0.458	0.5180	pH*Cue	106.572	1	106.562	0.095	0.7660
pH*Mass	1718.783	1	1718.783	0.568	0.4730	pH*Mass	496.104	1	496.104	0.422	0.5250
Cue*Mass	452.211	1	452.211	0.149	0.7090	Cue*Mass	773.293	1	773.293	0.689	0.4310
pH*Cue*Mass	6205.456	1	6205.456	2.051	0.1900	pH*Cue*Mass	561.588	1	561.588	0.501	0.4990
Within	24202.696	8	3025.337			Within	8976.000	8	1122.000		
Total	177335.145	15				Total	47511.498	15			
Shapiro Wilk test for normality p > 0.05 for all ANCOVAs Levene’s test for homogeneity of variances p > 0.05 for all ANCOVAs											

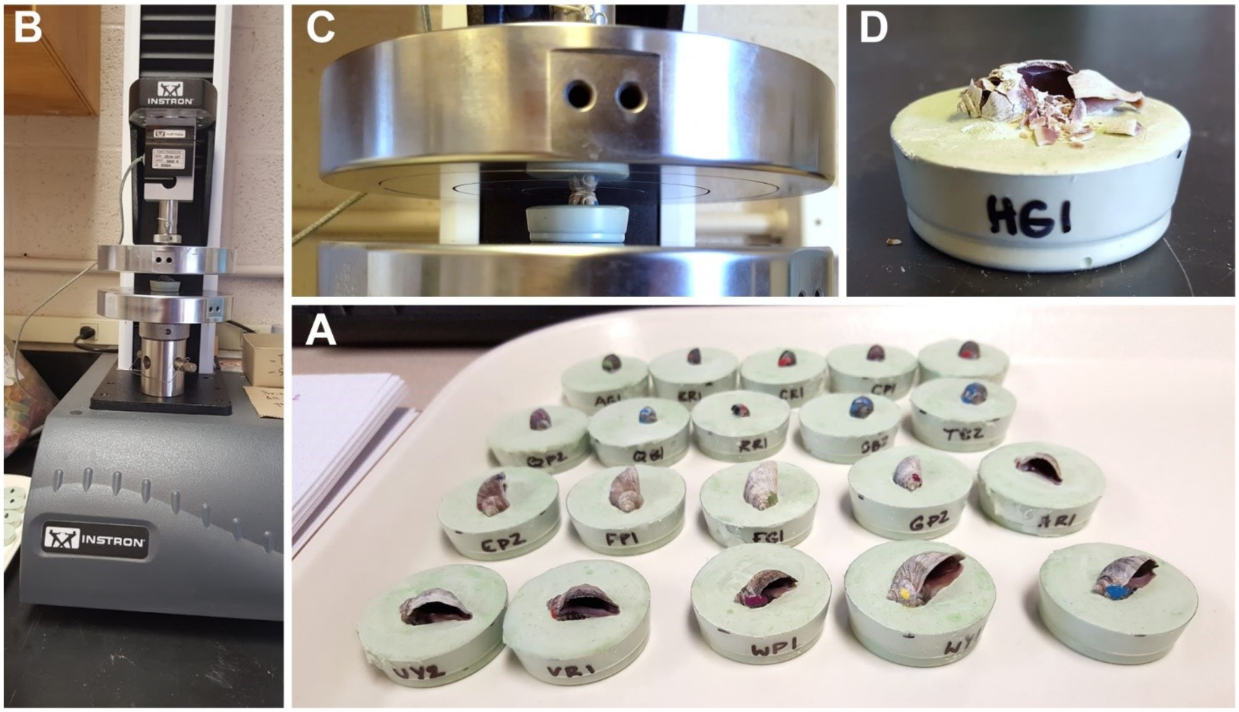

Figure 2.1

Photos of Instron® crushing tests. A. Prepared specimens. Specimens were placed in dental plaster plugs, aligned using a protractor, and placed with the outer apertural lip facing the upper plate of the Instron® and the axis of coiling parallel to the dental plaster/Instron® plates. **B. Photo of the Instron® universal testing system with a prepared shell between the plates.** The upper plate was placed immediately above the highest point of the shell and then lowered at a constant speed until the point of total shell failure. **C. Close up view of a specimen of *N. ostrina* during a crushing trial.** The orientation of the shell roughly simulated the manner in which a crab would initially attempt a static crush of the shell (squeezing the sides of the shell). **D. A specimen of *N. ostrina* after crushing.** Shells were crushed to the point of total failure, which was a consistent popping or blow-out of the apex/spire in both species.

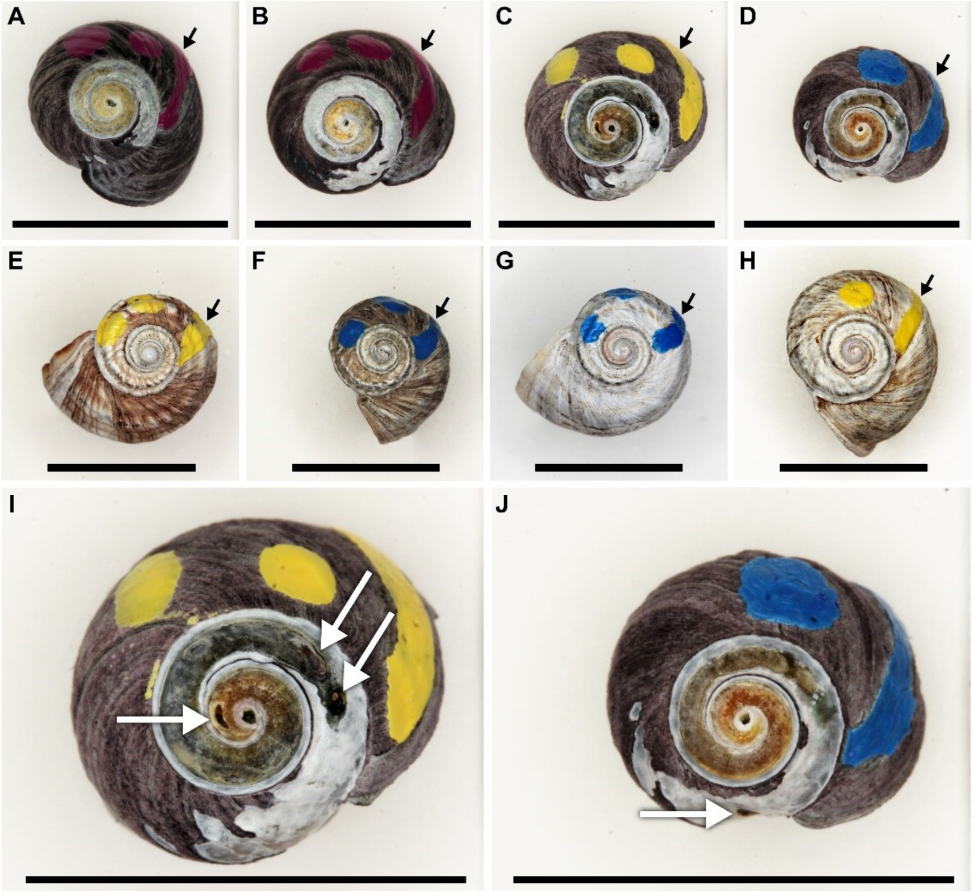

Figure 2.2

Apical-view photographs of representative gastropods from each of the eight experimental treatments. Scale bar is 1 cm in length. Nail polish lines along the body whorl (as indicated by black arrows on the upper right side of gastropod) indicate the leading edge of the shell and thus the gastropod's size at the beginning of the experiment. All subsequent growth (clock-wise from the nail-polish line) indicates growth under the six month experimental treatment. The nail polish was aligned at approximately the same angle for each specimen to allow easy visual comparison of shell growth. Colour and extra nail-polish dots were used for specimen identification during the experiment. **A – D. Specimens of *T. funebralis*.** A. Ambient, no cue. B. Ambient, cue. C. Low pH, no cue. D. Low pH, cue. **E – F. Specimens of *N. ostrina*.** E. Ambient, no cue, F. Ambient, cue. G. Low pH, no cue. H. Low pH, cue. **I. and J. Expanded images of C and D, respectively.** White arrows indicate dissolution and pitting of the *T. funebralis* shells experienced under low pH treatments, which often resulted in outright holes (horizontal white arrows in both I and J).

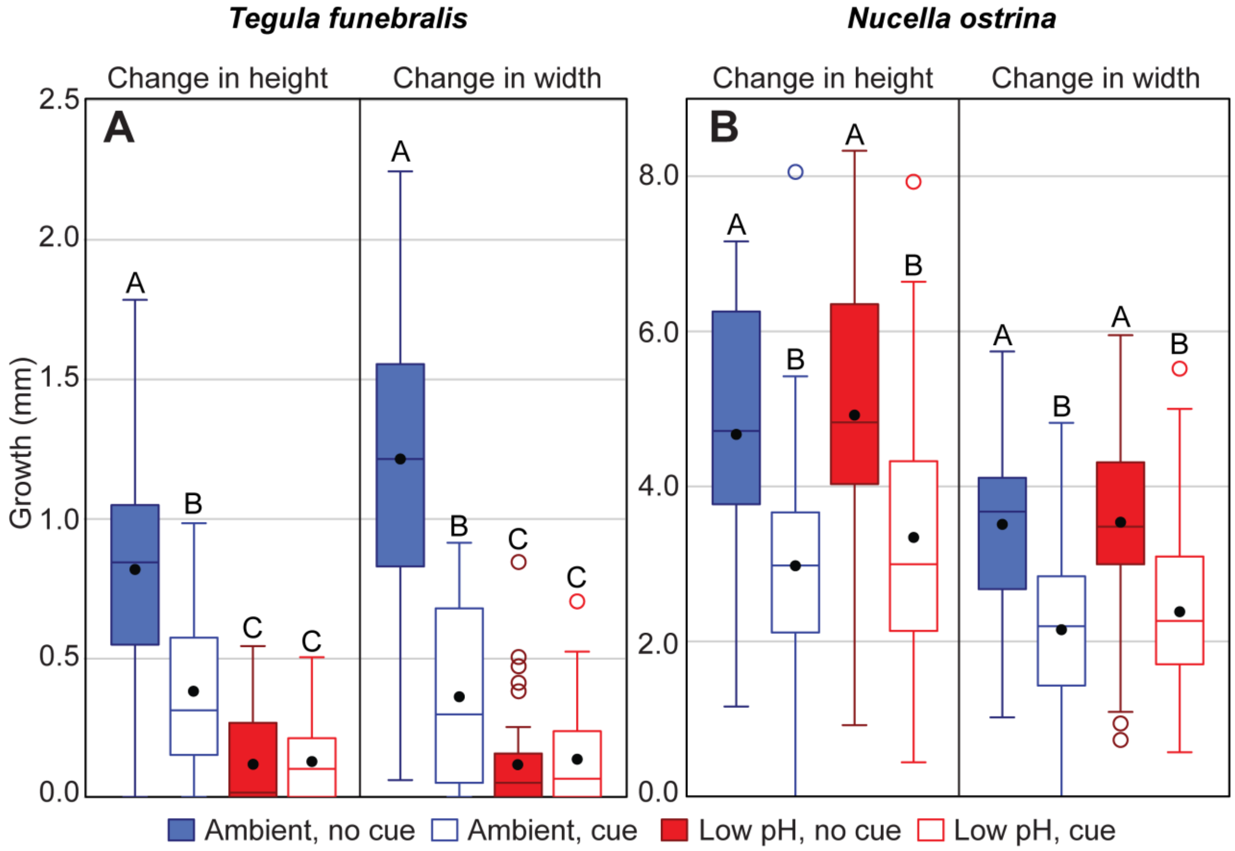

Figure 2.3

Boxplot of new shell growth of *T. funebralis* (A) and *N. ostrina* (B) over the 185-day experiment. Note that axes (mm) differ between panels (*N. ostrina* grew faster than *T. funebralis*). Each legend item indicates a treatment group (*n* =40 per species). Boxes indicate upper and lower quartiles, with central lines indicating medians, means as black circles, and letters indicating groups that differ significantly. Whiskers represent min/max data. Outliers are indicated by open circles.

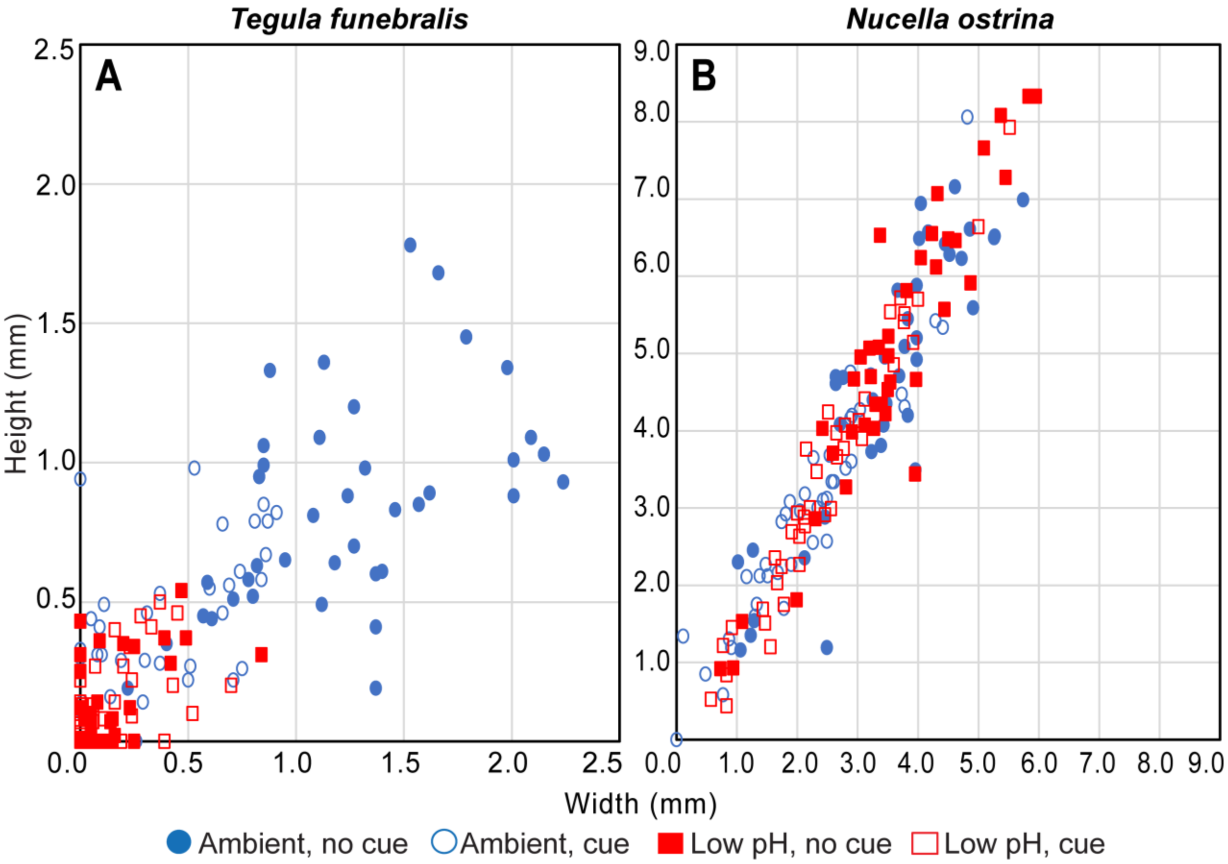

Figure 2.4

Scatterplot of new shell growth of *T. funebralis* (A) and *N. ostrina* (B) over the 185-day experiment. Note again that axes (mm) differ between panels. Each legend item indicates a treatment group (*n* =40 per species). Color indicates pH treatment. Solid shapes indicate treatments without a cue, and open shapes indicate those which had a cue. The scatterplots do not indicate any discernable changes to exterior shell morphology (height and width) caused by any of the experimental treatments.

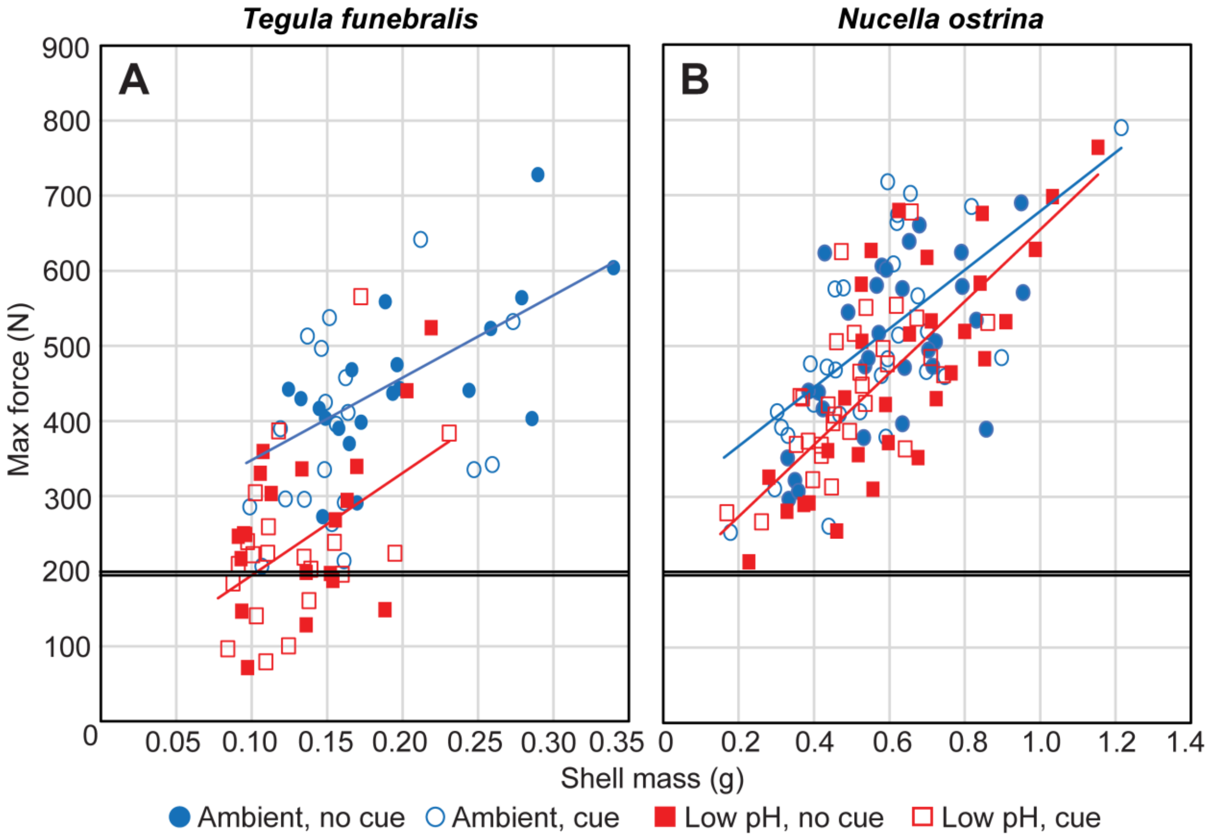

Figure 2.5

Shell strength of *T. funebralis* (A) and *N. ostrina* (B) after experimental treatments. X axes ranges are not constant between panels (*N. ostrina* grew larger than *T. funebralis* and therefore weighed more – *N. ostrina* specimens were approaching adult size at the end of the experiment). Mass (g) of dried shells was a proxy for size. Max force (N) values were recorded by the Instron® at total shell failure. Treatments are indicated by colour and shape (*n* =20 and 30 for *T. funebralis* and *N. ostrina* respectively). Blue (ambient) and red (low pH) trend lines indicate 95% confidence lines for pH treatments. The black line (200 N) indicates conservative crushing-force estimates for adult *Cancer productus* (Taylor 2000). As *N. ostrina* is often observed being crushed outright by crabs (e.g., Mendonca et al. 2017), this suggests that the max force values (y axis), and subsequent interpretation, are conservative.

Chapter 3

The role of gastropod shell composition and microstructure in resisting dissolution caused by ocean acidification

3.1 Introduction

Ocean acidification, caused by the absorption of increased atmospheric carbon dioxide in sea water, is expected to have detrimental effects on a wide variety of marine organisms by the end of the century (Orr et al. 2005; Gattuso et al. 2015; Pörtner et al. 2019). Organisms that secrete hard parts made of calcium carbonate have been shown to be particularly vulnerable, as their ability to both produce and maintain their shells is often negatively impacted by acidification (Barry et al. 2011; Ries 2011*a*; Kroeker et al. 2013; Byrne and Fitzer 2019). In particular, an organism's ability to maintain existing shell material is important for resisting predation, desiccation, and even parasitism or infection (Geller 1982*a*; Vermeij 1993). However, calcifying organisms produce their skeletons from carbonate materials that differ in energetic costs (Palmer 1983, 1992), as well as microstructure and composition (Watabe 1988), which may be variably susceptible to dissolution. In the following study, we examined shell microstructure and composition of two intertidal gastropods species that show contrasting responses to decreased seawater pH to determine how each shell type was affected. As shell composition and microstructure are often well established for calcifying organisms, particularly molluscs (Watabe 1988), understanding how shell types are affected by acidification may have far reaching implications for predicting the vulnerability of organisms to both past and future ocean acidification.

There has been enormous effort to understand how calcifying organisms and their ecosystems will respond to ocean acidification over the past two decades (Ries 2011*a*; Kroeker et al. 2013; Gaylord et al. 2015). Research has shown that even within taxonomic groups, such as the molluscs, not all species respond to acidification in the same manner, and some species are able to maintain, or even increase calcification under acidification (Ries et al. 2009; Findlay et al. 2011; Ries 2011*b*; Byrne and Fitzer 2019). Molluscs demonstrate biological control over calcification, using bicarbonate (HCO_3^-) and carbon dioxide (CO_2) rather than carbonate (CO_3^{2-}) in the calcification process (Findlay et al. 2011; Harvey et al. 2018, Byrne and Fitzer 2019, and references therein). As ocean acidification primarily affects the saturation of carbonate ions in seawater (Morse et al. 2007; Ries et al. 2009), it is possible that decreases in carbonate saturation itself may not affect calcification in organisms that are biologically able to control the site of calcification (Findlay et al. 2011), although hypercapnia would likely still be an added stress (Byrne and Fitzer 2019). However, existing calcified structures are still susceptible to dissolution if seawater becomes undersaturated in carbonates (Nienhuis et al. 2010; Queirós et al. 2015; Chatzinikolaou et al. 2017; Harvey et al. 2018). Therefore the ability to maintain existing structures or respond plastically to changes in carbonate saturation may become critical for molluscs as carbonate saturation decreases (Ries 2011*a*; Langer et al. 2014; Duquette et al. 2017; Leung et al. 2017*a*), particularly as shells provide protection against predators, parasites, and may also provide temperature regulation (Geller 1982*a*; Vermeij 1993). Understanding how shell materials are affected by corrosion could provide key insights on which organisms might be most vulnerable to ocean acidification both in the future, as well as during periods of potential carbonate undersaturation in the past, particularly as acidification has been invoked for several major extinction events (Kump et al. 2009; Kiessling and Simpson 2011; Greene et al. 2012; Honisch et al. 2012; Clarkson et al. 2015; Henehan et al. 2019).

Most calcifying organisms create their shells from one of two carbonate ($CaCO_3$) polymorphs: calcite and aragonite. Aragonite contains more magnesium (Mg), which produces weaker bonds in the crystalline structure, and is therefore more soluble/prone to dissolution (Morse et al. 2007). Low-Mg calcite is more stable and resistant to dissolution, becoming more soluble as the magnesium content increases (e.g., high-Mg calcite shells) (Ries 2011*a*). Those organisms which have increased magnesium content in their skeletons, such as aragonite, are expected to be more vulnerable to dissolution under future ocean conditions (Ries 2011*a*). However, some organisms may possess at least partial control over the magnesium to calcium ratio (Mg/Ca) in their shells, and plastically respond to changes in water chemistry by decreasing the Mg/Ca ratio of their skeletons (Ries 2011*a*; Leung et al. 2017*b*).

Organisms also vary in the microstructural arrangement of their skeletons, as well as the organic content of those microstructures. Molluscs in particular have distinct shell types that may be distributed widely across taxonomic groups. Shells typically occur as layers that vary in both which carbonate polymorph is used to make the layer, as well as the crystalline structure of that layer. For example, many species of molluscs possess nacre (mother of pearl) made of stacks of flat aragonite crystals with considerable organic matrix on which the crystals formed (Watabe 1988). Nacre has the advantage of being mechanically stronger than other shell types (Currey 1988), but given the high organic content, it is also more energetically costly to produce (Palmer 1983, 1992). In contrast, some mollusc species possess a homogenous layer made of small, granular crystals of calcite or aragonite, containing little organic matrix (Watabe 1988), which is mechanically weaker, but far cheaper to produce (Palmer 1983; Currey 1988; Avery and Etter 2006). Some species can increase the thickness of this cheaper homogenous layer under threat of predation (Avery and Etter 2006). As mentioned previously, some gastropod species also exhibit similar plastic responses to increased acidification, and preferentially thicken specific shell layers (Langer et al. 2014), or increase production of cheaper polymorphs (Leung et al. 2017*a*).

Given the costs of producing more complex structures with more organic matrix (Palmer 1983), such as nacre, it has been suggested that organisms with higher aragonite and/or organic content in their shells will be more vulnerable to acidification (Ries 2011*a*; Leung et al. 2017*b*, *a*). Not only does organic matrix indicate increased costs for production, but organic matrix may also exacerbate dissolution by promoting bacterial decay (Harper 2000). In addition to organic content, the shape, size, and orientation of crystals, particularly crystal edges, may act as additional surface area on which dissolution might occur (Harper 2000). For example, some molluscs possess an outer fibrous prismatic layer with thin, elongate crystals oriented perpendicular to the shells surface, exposing many small crystal faces and edges, rather than other shell types where fewer, larger crystal surfaces are exposed (Harper 2000). Furthermore, Harper (2000) found that crystal size and orientation was more important to resisting dissolution than carbonate polymorphs, with calcite prisms being more prone to dissolution than some forms of nacre. Here, in addition to shell composition, we explore potential relationships between intercrystalline crystal size/orientation, surface area and dissolution.

Along rocky shores of the northeastern Pacific, the gastropods *Tegula funebralis* and *Nucella ostrina* are ubiquitous members of rocky intertidal communities. Ocean acidification has become of particular concern within their habitat, particularly in California, as upwelling along the California Current system exacerbates acidification in nearshore environments (Feely et al. 2008, 2016; Chan et al. 2017; Pörtner et al. 2019). Both gastropods are common prey for shell-crushing predators, such as cancrid crabs (Geller 1982*b*, 1983; Mach and Bourdeau 2011; Bourdeau 2013; Molinaro et al. 2014; Stafford et al. 2015*a*; Mendonca et al. 2017; Tyler et al. 2019). As shells are a vital means of passive defense against predation, both species' abilities to maintain their shells and resist dissolution may alter their vulnerability to predators as carbonate saturation states continue to decrease. In addition, the shell microstructures observed in both species are also seen in many other molluscs, which means that the effects observed in either species could have broader implications for other molluscs with similar microstructures.

Tegula funebralis (Trochoidea) has a shell comprised of two layers: an outer fibrous prismatic layer with thin, elongate crystals arranged perpendicular to the shell surface, and an inner nacreous layer (Geller 1982*a*). Erosion of the purple-black fibrous prismatic layer is fairly common in adults, particularly near the apex, and is caused by a combination of fungal and algal growth which exacerbates normal abrasion of the shell (Geller 1982*a*). *T. funebralis* often secrete a thin cross-lamellar aragonite layer at spots where erosion has been extensive, sometimes appearing as an orange or greenish layer underneath the nacreous layer (Geller 1982*a*). The second species, *Nucella ostrina* (Muricoidea) has a shell comprised of an outer homogenous layer of calcite (Nienhuis et al. 2010), and an inner layer of cross-lamellar aragonite (Avery and Etter 2006).

In a previous study, we examined the responses of *T. funebralis* and *N. ostrina* to long-term exposure to decreased seawater pH (Barclay et al. 2019). Juveniles of both gastropods were exposed to low pH conditions for six months, and their response was measured as a function of changes to both shell growth and strength. *T. funebralis* showed significant reductions in both shell growth and strength, whereas *N. ostrina* was able to maintain its growth, but still experienced a 10% reduction in shell strength (Barclay et al. 2019). Here, we focus mostly on the observed changes to shell strength as it relates to dissolution of existing material. The results of the previous study (Barclay et al. 2019) match the prediction that shells with greater aragonite and organic content (e.g., *Tegula*) experience greater costs under decreased seawater pH than those with more calcite. Other studies of *Nucella* species have also found that calcification is maintained under decreased pH, and have found that the shells experienced dissolution (Nienhuis et al. 2010; Queirós et al. 2015; Rühl et al. 2017). However, without examining the shell structure of both species in more detail, it is unclear how these responses manifested in either of the species studied, or whether reductions in strength are due to dissolution. For example, other species of *Nucella* exhibit plasticity of their shell layers, where those exposed to increased predation pressure preferentially thicken the cheaper, but weaker, homogenous layer as a means of increasing shell size (Avery and Etter 2006). In addition, the composition of the outer fibrous prismatic layer in *T. funebralis* has not been described explicitly.

Here we examine shell microstructure and composition of *T. funebralis* and *N. ostrina* to determine the effects of shell type and potential dissolution on their shell integrity. Shells from a previous experiment where both species were exposed to either ambient or decreased pH water conditions for six months to determine the effects of acidification on shell growth and strength (Barclay et al. 2019) were used in the following study to examine shell density, composition, and microstructure. We use a combination of microCT scans to assess changes in shell density, XRD analyses to examine changes to calcite and aragonite composition, and SEM imaging to examine the microstructure of the shells in detail. Our goal was to determine the role of shell microstructure and composition in resisting potential dissolution caused by ocean acidification.

3.2 Methods

3.2.1 Experimental Conditions

We exposed juveniles of *T. funebralis* and *N. ostrina* to reduced pH seawater conditions for a period of six months in a previous experiment at Bodega Marine Laboratory (Barclay et al. 2019). 80 individuals of both *T. funebralis* and *N. ostrina* were collected and allowed to acclimate for three weeks before beginning laboratory experiments. In the original experiment, there were two additional treatments (another 80 individuals of each species) where both species were exposed to crushed conspecific cues (Barclay et al. 2019), but here, we focus exclusively on non-cue treatments, so as to examine potential effects caused exclusively by differences in pH. Low pH treatments were manipulated daily to maintain a consistent drop of 0.5 pH units (total scale) compared to control (ambient) treatments. Ambient seawater was collected from the incoming water supply, with low pH treatments created through direct chemical manipulation by adding equimolar parts of 1 M hydrochloric acid (HCl) and sodium bicarbonate ($NaHCO_3$), as outlined by international standards for simulating the effects of increased atmospheric CO_2 in seawater (Riebesell et al. 2010). There were 4 replicate treatment tanks per species and treatment, with 10 individuals per tank (40 individuals of each species per treatment). After six months, individuals were humanely euthanized by freezing for 24 hours, and the body tissue was carefully removed. Shells were then weighed, and specimens were selected randomly for biomechanical tests (n = 20 and 30 per treatment for *T. funebralis* and *N. ostrina*, respectively). Shell strength of each individual was measured as the maximum force (N) required to crush each shell to the point of total failure (blowing-out of the spire) using an Instron® universal testing system. Analysis revealed that regardless of size (shell mass), shells of *T. funebralis* and *N.*

ostrina were 50% and 10% weaker, respectively, under low pH conditions. For further experimental details and accompanying data, please see the text and supplemental materials of Barclay et al. (2019). The remaining shells from each treatment that were not destroyed in the biomechanical tests (n = 20 and 10 per treatment of *T. funebralis* and *N. ostrina*, respectively) were put in sealed containers and brought back to the University of Alberta for further analysis of the shell microstructure and composition, which is the focus of this study.

3.2.2 Shell Density: MicroCT

To examine any changes in shell density that would explain the loss in strength observed in shells from low pH treatments, specimens were scanned using micro-computed tomography. For each treatment, 1 specimen from each replicate tank was selected randomly for scanning (4 ambient and 4 low pH per species, 16 scans total). Scans were performed using a SkyScan™ 1172 microCT scanner (Bruker, Belgium) and for each species, scans were conducted back to back in random order using the same settings to ensure scans were comparable and drift of the machine did not affect the results. Specimens were scanned through a half rotation (180º) at a magnification of 6.5 µm at a resolution of 4000 x 2096 pixels with a voltage of 70 Kv and a current of 142 µA, and using an aluminum 0.5 mm filter. Completed scans were then reconstructed using the NRecon software package (SkyScan™) which uses a modified Feldkamp's back-projection algorithm (Feldkamp et al. 1984). For each species, all reconstructions were performed using the same reconstruction parameters (beam hardening, ring artefact reduction, attenuation coefficients) to ensure that the scans were directly comparable. Once the scans were reconstructed, they were opened in DataViewer (SkyScan™) and rotated so that the coiling axis of the shell was in a vertical position. From there, 12 cross-sections of preselected representative areas of the shell (three from each of the apex, spire (just above the body whorl), mid body whorl, and lip) were selected for analysis of greyscale values (density). As dissolution was expected to occur on the external surface, for each selected slice, a band of the external shell surface was selected for analysis. Each image was edited in ImageJ, where a 15 pixel-wide band was created along the external edge of the shell to be used in analyses, following the methods of Queirós et al. (2015), except in the case of the lip area, where the shell was thin enough to include the entire section. The mean greyscale values of each section were then determined using the binary threshold module (1 – 255 greyscale histogram range) in the program CTAnalyser (SkyScan™), with higher greyscale values indicating greater density of the shell materials. Visual comparison of the density of the slices was facilitated by adding a 16-bit colour scheme to the cross-sectional images. The slices were loaded into DataViewer and the Color 2 module was applied, with warm colours indicating areas of higher density, and cool colours indicating areas of lower density. Shell quality and overall appearance (such as jagged edges indicating dissolution) were also noted.

3.2.3 Shell Composition: XRD

To determine if pH treatments affected the aragonite or calcite content of the shells, specimens were analysed using X-ray diffraction. Another specimen from each tank (not those used for microCT scanning) was selected randomly (4 ambient, 4 low pH per species, 16 total). For each specimen, the shell was broken and the fragments were ground into a powder using a mortar and pestle that had been cleaned with silica and wiped with ethanol. Shell fragments were ground using 95% ethanol to prevent loss of shell powder as well as any changes to aragonite due to the action of grinding. The ethanol was allowed to evaporate, and sample powders were loaded onto zero-background plates. Specimens were then analysed using a Rigaku Ultima IV scanner with a Cobalt tube at 38 kV and 38 mA. Scans were conducted from 5 – 90º 2ϴ with a step size of 0.020º at a speed of 2º/min. Data interpretation was done using JADE 9.6 software with the 2019 ICDD Database PDF 4+, and 2018-1 ICSD databases. The % calcite content of each sample was determined as (Ic/Ic+a), the ratio of the primary calcite peak height (d_{104} = 3.036 Å: 34.30°2θ) to the sum of the primary calcite peak height and primary aragonite peak heights (d_{111} = 3.396 Å: 30.57°2θ; d_{021} = 3.273 Å: 31.74°2θ). The % aragonite was simply taken as the difference of the % calcite from 100%.

3.2.4 Shell Microstructure: SEM

Microstructure and shell quality of the specimens was assessed visually under SEM. A broken fragment of the outer shell lip from one specimen per treatment (those used in XRD analysis) were gold sputter-coated and observed under a Zeiss Sigma 300 VP field emission scanning electron microscope. Cross-sectional images of the broken surfaces were used to observe microstructure and assess shell quality. The external surfaces of the shell fragments were also imaged to observe any changes to shell quality between the treatments.

3.2.5 Analyses

To determine if density of the microCT slices was affected by pH, greyscale values were compared using a generalized linear mixed model (family = gaussian) for each species, with pH as a fixed effect and individual and sections/slice as random effects. Mixed models can be used to address pseudoreplication within study design, such as the number of slices and individuals within treatments, by allocating random effects for those variables that might show pseudoplication. To determine if one species was affected more than the other, we ran an additional model including both species, where species was added as an additional fixed effect and crossed with pH to test for an interactive effect between species and pH. The performance of the models was tested by using log-likelihood comparison tests against a null (intercept-only) model, with the best models in each pair having lower Akaike Information Criterion (AIC) scores. The significance of pH and species (and their interaction) on density was then explored using t-values.

Calcite:aragonite ratios from XRD analyses were compared between treatments using a two-tailed Welch's t-test (assuming unequal variances) for each species. The need for a mixed model was unnecessary to compare the XRD samples, as the analyses were run on whole individuals, and there were no random effects/pseudoreplication. All analyses were conducted using R v3.4.4.

3.3 Results

3.3.1 Shell Density

The fitted models performed significantly better than a null model ($p < 0.0001$), indicating that pH affected shell density. Shell density was significantly decreased by exposure to low pH treatments in both species ($p < 0.001$) (Table 3.1, Fig. 3.1). Regardless of treatment, *N. ostrina* shell edges were significantly denser than the outer edges of *T. funebralis* shells ($p< 0.001$) (Table 3.1). The effects of pH also showed a significant interaction with species ($p = 0.038$), with *T. funebralis* shells becoming 14 – 25 % less dense under low pH conditions, compared to 8 – 11% reductions in density in *N. ostrina* (Table 3.1). When looking at the raw data, both species also showed the smallest changes in density in the newer parts of the shell (lip, 14 and 8 % respectively) (Table 3.1). The apical slices in *T. funebralis* had the largest differences in density between treatments, where slices from the low pH treatments were 25% less dense than those from the ambient treatments. In contrast, *N. ostrina* showed fairly uniform effects of dissolution (~10%) from all shell regions, except the lip (8% reduction in density) (Table 3.1).

Visual comparisons of the cross-section microCT images also indicated increased dissolution in those individuals exposed to low pH treatments, with specimens from low pH treatments showing cooler colours indicative of dissolution along the external shell surfaces than those from ambient treatments (Fig. 3.2). The separation of the outer fibrous and inner nacreous layers of *T. funebralis* was also easily distinguished in microCT cross-section by a brighter-coloured line on the images (Fig. 3.2), and it was clear that this nacreous material had a greater density than the outer layer. There was noticeable deterioration of the outer fibrous layer in low pH exposed *T. funebralis* specimens, marked by cooler colours and a jagged outline, with the outer layer completely missing in some areas of the shell. In both species, the cross sections of low pH specimens also appeared thinner in certain places (Fig. 3.2), although thickness measurements were not collected given the inconsistent distribution of these thinner portions of the shell (patchy rather than uniform thinning). The patchy wear in *T. funebralis* cross sections could also be recognized in whole specimens via increased exposure of the nacreous layer and under SEM as pitting on the surface of the shells (Fig. 3.3B). In general, the inner nacreous layer of *T. funebralis* was denser (warmer colours) than *N. ostrina* shells (Fig. 3.2), as would be expected given than nacre is made of aragonite and therefore denser than the homogenous calcite found in *N. ostrina* specimens.

3.3.2 Shell Composition

Shells of *T. funebralis* decreased in calcite content from ambient to low pH treatments (t-test, t = 3.674 p = 0.017). Under ambient conditions, calcite content ranged from 53 – 65%, but decreased to 31 – 45% in low pH treatments (Table 3.2). As the nacreous layer is made of aragonite, calcite content must have come from the outer fibrous layer, as is typical for many other trochoids and vetigastropods (Gainey and Wise 1980). Therefore, the loss of calcite content in low pH treatments must have been due to the dissolution and erosion of the outer shell layer observed in the cross-sectional microCT images and in whole specimens.

N. ostrina shells were mostly calcite (92 – 97%) and showed no significant changes in polymorph ratio under low pH treatments (t-test, t = 0.810, p = 0.465) (Table 3.2). Under SEM, the cross-lamellar layer (aragonite) (Fig. 3.3H) was thin compared to the homogenous calcite layer (~30 µm vs. ~300 µm), indicating that regardless of pH, *N. ostrina* shells are mostly comprised of the outer homogenous calcite layer, which corresponds to the XRD analyses.

3.3.3 Shell Microstructure

SEM imaging indicated signs of dissolution in specimens of both species exposed to low pH treatments, with increased pitting and/or rougher external surfaces (Fig. 3.3A-D). Signs of shell deterioration appeared mostly near the external shell surface, although there was some patchy deterioration of the inner nacreous layer of *T. funebralis* (Fig. 3.3G). External surfaces of both shells also showed some small circular holes/pitting, although this was more extensive in *T. funebralis*, extending down into the fibrous layer (Fig. 3.3E, F). In *T. funebralis*, there were also some round "spheres" less than 1µm in diametre, often found associated with the circular pitting, that have been attributed to a possible cyanophyte or other prokaryote (Geller 1982*a*) (Fig. 3.3E, F). These “spheres” were more extensive in *T. funebralis* from the low pH treatment, although they have been known to vary in density between specimens (Geller 1982*a*).

3.4 Discussion

Dissolution of calcified structures is likely to pose a major threat to shelled organisms as acidification of our oceans continue. Even for those species that appear to maintain calcification and growth, such as *Nucella ostrina*, the abiogenic loss of carbonate material due to dissolution in undersaturated waters will weaken shells, increasing the vulnerability of those organisms to predation (Barclay et al. 2019). The ability of shell materials to resist dissolution may therefore predict an organism’s vulnerability to ocean acidification. While the general assumption is that organisms with more calcite content will experience less dissolution, as calcite is less soluble than aragonite, we suggest that the microstructural arrangement of crystals in mollusc shell material also affects the extent of dissolution, in agreement with Harper (2000).

Corrosion of shell material has several potential negative consequences for calcifying organisms, such as gastropods. The most notable and widely discussed consequence is potential vulnerability to predation (Kroeker et al. 2014; Chatzinikolaou et al. 2017; Leung et al. 2017*b*; Harvey et al. 2018). The loss of shell material due to dissolution has been demonstrated in a number of gastropods, including other species of *Nucella* (Nienhuis et al. 2010; Queirós et al. 2015; Rühl et al. 2017). Our results suggest that dissolution is the most likely cause for the reduced shell strength observed in both species. In addition, the greater extent of dissolution observed in *T. funebralis* compared to *N. ostrina* (14 – 25% vs. 8 – 11% density reductions, respectively) corresponds with our previous study of shell strength, where *T. funebralis* suffered a greater loss of shell strength in *T. funebralis* (50%) than *N. ostrina* (10%) (Barclay et al. 2019). *T. funebralis* are much more mobile when exposed to crab effluent (Mendonca et al. 2017), and appear to rely on their shells, which are mechanically stronger than *N. ostrina* shells (Barclay et al. 2019), to resist crab predation, whereas *N. ostrina* attempt to avoid detection (Mach and Bourdeau 2011; Mendonca et al. 2017). As *T. funebralis* shells are weaker under increased acidification (Barclay et al. 2019), and decreased seawater pH can also hamper their ability to detect predators (Jellison et al. 2016), their reliance on their ability to resist crushing once caught will no longer be a favourable strategy. Not only may dissolution decrease shell strength, but the sometimes patchy dissolution, particularly in *T. funebralis*, may make both gastropods even more vulnerable, as such thinner or more dissolved parts of the shell may present points of weakness against shell crushing predators. For example, a predator may only need to break through one portion of the shell to gain access to the gastropod flesh. Dissolution may also increase the likelihood of fracture propagation, particularly in the homogenous layer, where fracture propagation is already more likely than in other layers (cross-lamellar or nacre), which are better at dissipating fractures (Currey 1988; Avery and Etter 2006).

Another suggestion has been than older parts of shells, such as the apex of gastropods, might experience more extensive dissolution, as these parts have been exposed to the unfavourable water conditions for longer (Chatzinikolaou et al. 2017; Harvey et al. 2018). In *T. funebralis,* the apices experienced the most dissolution (Table 3.1, Fig. 3.1). For both species in our study, there was less dissolution on the newest parts of the shell, with dissolution appearing more extensive on older portions of the shell (Table 3.1, Fig. 3.1). However, dissolution was fairly consistent in *N. ostrina*, particularly between the apex, spire, and whorl, with only slightly less dissolution of the lip (8% instead of 10 – 11%), so dissolution may occur more evenly in *N. ostrina*. Where dissolution is extensive enough to develop holes, organisms may become even more vulnerable to risks such as predation, desiccation, or disease (Geller 1982*a*). In the case of *T. funebralis*, the apex area was often much more eroded in low pH treatments than in ambient, and several specimens from low pH treatments developed holes visible to the unaided eye (Barclay et al. 2019) (Fig. 2.2I, J). While erosion of the apex is typical for *T. funebralis* (Geller 1982*a*), it appears that dissolution in the low pH treatments only exacerbated this deterioration of the apex.

Both *T. funebralis* and *N. ostrina* possess an outer shell layer made of calcite, which in theory should act as a buffer against dissolution when compared to aragonite. However, *T. funebralis* experienced more extensive dissolution, particularly of the calcite layer. The loss of calcite content in *T. funebralis* from low pH treatments (XRD analyses) may at first seem counterintuitive if we expect aragonite (i.e., the nacreous layer) to be more susceptible to dissolution. But, corrosion of the shell occurs more extensively on external exposed surfaces, suggesting that the increase in aragonite content in *T. funebralis* from low pH treatments is simply a reflection of the loss of the outer calcitic layer, which we also observed in cross sectional images of the microCT scans, and when looking at whole specimens (more extensive exposure of the inner nacreous layer).

There are several possible explanations for the increased dissolution observed in *T. funebralis* over *N. ostrina.* The latter might have benefitted from having a thicker calcitic layer than *T. funebralis*. Indeed, there were several cross-sectional images where the outer calcite layer in *T. funebralis* had been completely removed in places (Fig. 3.2), leaving the more susceptible nacreous (aragonitic) layer exposed. However, our measurements of density were based on a band created from the external surface of the shell, including the denser nacreous layer of *T. funebralis* in spots where the outer layer had been removed. The increased dissolution observed in *T. funebralis* is likely a conservative result as, if anything, the inclusion of the denser nacreous layer in places where the calcitic layer had been removed probably weakened our density results. Therefore, it appears that thickness of the outer layer alone is insufficient to explain why *N. ostrina* was more resistant to dissolution, as despite having outer layers made of calcite, the outer layer of *T. funebralis* was more susceptible to dissolution than that of *N. ostrina*.

Compared to *N. ostrina*, increased dissolution of the outer calcite layer in *T. funebralis* could be caused by the microstructural arrangement of the calcite crystals. The outer fibrous layer in *T. funebralis* has more crystal edges that could become exposed, with larger surfaces on which dissolution might occur. In contrast, the outer homogenous layer of *N. ostrina* has small, grainy crystals that are more closely spaced, potentially decreasing the surface area on which dissolution might occur. Even in ambient conditions, the density of the outermost part of *N. ostrina* shells was greater than in *T. funebralis*. Furthermore, while organic matrix itself can increase resistance to dissolution, this is only true in sterile conditions, as bacterial decay of the organic matrix can increase rates of dissolution (Harper 2000). It is therefore possible that the increased organic content in *T. funebralis* compared to *N. ostrina*, particularly between crystals, could expose additional surfaces that might exacerbate dissolution in seawater. In other studies of bivalves, homogenous layers made of aragonite were less susceptible to dissolution than fibrous prismatic calcitic layers, suggesting that microstructural arrangement was more important to resisting dissolution than carbonate polymorphs (Gabriel 1981; Harper 2000). Here, we support those results in gastropods, even when the carbonate polymorph is the same between microstructures. As fibrous prismatic calcite layers appear in other groups, such as the Mytilidae (mussels) and Pectinidae (scallops) (Watabe 1988), and still appear more susceptible to dissolution than other shell types in both bivalves and gastropods, this suggests that dissolution of microstructures is consistent across molluscs, and that fibrous prismatic layers are more prone to dissolution than homogenous layers.

However, *T. funebralis* typically shows extensive erosion not normally observed in other molluscs. This erosion, particularly of the apex, is caused by fungal/algal growth that consumes the organic matrix (Geller 1982*a*). Therefore, it is possible that the increased dissolution of the calcite layer in *T. funebralis* was at least in part exacerbated by the loss of protective organic matrix consumed by fungal/algal growth, resulting in exposure of a larger surface area of the crystals. But as other molluscs that also have a fibrous prismatic calcite layers also show more dissolution even than taxa with homogenous layers made of aragonite (Harper 2000), we suggest that microstructural arrangement still likely plays a significant role in resisting dissolution. *T. funebralis* may be especially vulnerable to the effects of ocean acidification, due both to the increased rates of dissolution of the fibrous prismatic calcite layer and consequent exposure of the more vulnerable nacreous layer, as well as to the loss of organic matrix caused by fungal/algal growth, leading to increased dissolution of all exposed parts of the shell.

From both the cross-sectional images of the microCT scans and SEM, as well as the results of the XRD analyses, there does not appear to be a plastic response in either species, in terms of their shell construction, to ocean acidification. There was no thickening of layers in either species, with dissolution simply reducing overall shell density/quality, and in some places, shell thickness. Dissolution occurred primarily on the shell surface, with some more extensive pitting and erosion of the outer fibrous layer in *T. funebralis*. As *N. ostrina* shells were primarily made of a homogenous calcite layer, the need for a plastic response might have been unnecessary, as the microstructure is already "optimized" for resisting dissolution as much as possible for the species. Furthermore, in earlier experiments on *N. ostrina,* there was no plastic thickening of the shells when exposed to crushed conspecific (predation) cues (Barclay et al. 2019), even though plastic responses are known for other species of *Nucella* (Appleton and Palmer 1988; Avery and Etter 2006; Bourdeau 2012), suggesting that *N. ostrina* might not be capable of plastically responding (Bourdeau 2010*b*, but see Pearson 2004). We suggest this inability to respond to acidification plastically might be unnecessary due to the extensive thickness of the calcitic layer, which comprised over 90% of the shell, compared to other species of *Nucella* which have thicker inner cross-lamellar layers (Avery and Etter 2006; Nienhuis et al. 2010). Other studies of shell thickening in *N. ostrina* exposed to predation cues have found that this response is simply a by-product of reduced growth rates, rather than a plastic response (Bourdeau 2010*b*). *T. funebralis* shells are also not known to respond to changes in environmental conditions or the threat of predation plastically (Geller 1982*b*; Jacobsen and Stabell 2004; Barclay et al. 2019), presumably because of the increased energetic costs in producing their shells (Palmer 1992).

Overall, our results suggest that *N. ostrina* will be better equipped to face increased ocean acidification due to the microstructure and composition of its shell. *T. funebralis* will be more vulnerable not only given the increased energetic costs required to grow its shell, but also due to the arrangement of its microstructure, regardless of carbonate polymorphs. Fibrous prismatic layers, as seen in *T. funebralis*, appear more susceptible to dissolution than other microstructures, at least among the types observed in the present study. *T. funebralis* might also be particularly vulnerable given that fungal/algal growth consumes the organic matrix that otherwise protects shell crystals from exposure to dissolution. Our results are consistent with other reports of microstructural chemical resistance in bivalves and other gastropods (Gabriel 1981; Harper 2000), suggesting that the results of microstructural studies in specific taxa can be applied broadly across molluscs. As dissolution will likely affect all shell compositions as carbonate saturation states continue to decrease, microstructure can be used as a means of assessing species vulnerability to ocean acidification.

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Table 3.1

Mixed model summary results and summary data for exterior band shell densities (average greyscale values) in *T. funebralis* and *N. ostrina*. Log-likelihood comparisons of null (intercept only) models to full models (fixed effects = pH, species, random effects = individual, slice). Lower AIC scores indicate the better model in each pair (*T. funebralis* only, *N. ostrina* only, and both species). Summary data for densities of the four shell areas used, along with the % density reduction for each section under low pH, are included below mixed model results. Density values are based on average greyscale values for each shell band (± SD) with greater values indicating greater densities.

Mixed models of shell density (family = gaussian)								
Tegula funebralis								
Model	**AIC**	**BIC**	**logLik**	**Resid. Df**	**Resid. Dev**	**Chisq**	**Chi DF**	**Pr(>Chi)**
Null	700.1	710.4	-346.1	92	692.1			
pH	**683.0**	**695.8**	**-336.5**	**91**	**673.0**	**19.156**	**1**	**<0.0001**
				Random effects		**Name**	**Variance**	**Std. Dev**
				Individual		(Intercept)	4.572	2.138
				Slice		(Intercept)	29.359	5.418
				Residual			55.260	7.434
			Fixed effects		**Estimate**	**Std. Error**	**t value**	**Pr (>|t|)**
			Intercept		117.792	3.104	37.950	**<0.0001**
			pH		-20.243	2.142	-9.450	**<0.0001**
Nucella ostrina								
Null	631.7	642.0	-311.9	92	623.7			
pH	**621.5**	**634.3**	**-305.7**	**91**	**611.5**	**12.245**	**1**	**0.0005**
				Random effects		**Name**	**Variance**	**Std. Dev**
				Individual		(Intercept)	8.838	2.973
				Slice		(Intercept)	64.695	8.043
				Residual			25.520	5.052
			Fixed effects		**Estimate**	**Std. Error**	**t value**	**Pr (>|t|)**
			Intercept		138.548	4.349	31.857	**<0.0001**
			pH		-13.240	2.341	-5.655	**0.0007**
Both species								
Null	1412.2	1425.2	-702.1	188	1404.2			
pH*Species	**1368.5**	**1391.3**	**-677.3**	**185**	**1354.5**	**44.272**	**2**	**<0.0001**
				Random effects		**Name**	**Variance**	**Std. Dev**
				Individual		(Intercept)	4.458	2.111
				Slice		(Intercept)	28.245	5.315
				Residual			60.434	7.774
			Fixed effects		**Estimate**	**Std. Error**	**t value**	**Pr (>|t|)**
			Intercept		138.548	3.072	45.106	**<0.0001**
			pH		-13.240	2.179	-6.077	**<0.0001**
			Species		-20.756	2.179	-9.526	**<0.0001**
			pH*Species		-7.003	3.081	-2.273	**0.0380**

Density summary data							
		T. funebralis			***N. ostrina***		
		Average	**SD**	**% Density loss**	**Average**	**SD**	**% Density loss**
Apex	**Ambient pH**	114.38	6.94		137.67	3.99	
	Low pH	85.54	8.12	25.22	124.35	8.99	9.68
Spire	**Ambient pH**	113.11	5.02		137.12	5.94	
	Low pH	96.48	4.77	14.70	122.83	5.33	10.42
Whorl	**Ambient pH**	121.75	9.21		128.99	4.59	
	Low pH	102.91	7.79	15.47	115.38	5.74	10.55
Lip	**Ambient pH**	121.93	6.63		150.42	3.94	
	Low pH	105.27	9.53	13.67	138.68	7.08	7.80

Table 3.2

Results of XRD analysis in *T. funebralis* and *N. ostrina*. Calcite content was determined as the ratio of the primary calcite peak (d_{104} = 3.036 Å: 34.30°2θ) to the sum of the primary aragonite peaks (d_{111} = 3.396 Å: 30.57°2θ; d_{021} = 3.273 Å: 31.74°2θ), or (Ic/Ic+a). Aragonite content was taken as 100% - calcite content, and then the calcite:aragonite ratio was calculated for use in Welch's t-tests for each species.

XRD results (calcite and aragonite content)						
	C d_{104}	**A d_{111}**	**A d_{021}**	**% Calcite**	**% Aragonite**	**Calcite:Aragonite**
T. funebralis						
Ambient pH	12359	7158	3763	53.09	46.91	1.1317
Ambient pH	15380	7746	4454	55.77	44.23	1.2607
Ambient pH	17368	9105	5053	55.09	44.91	1.2267
Ambient pH	23734	8158	4550	65.13	34.87	1.8676
Low pH	12372	9697	5216	45.34	54.66	0.8296
Low pH	9339	9643	5427	38.26	61.74	0.6197
Low pH	10247	8379	4379	44.54	55.46	0.8032
Low pH	9049	12835	7212	31.10	68.90	0.4514
N. ostrina						
Ambient pH	52422	1808	151	96.40	3.60	26.7596
Ambient pH	41695	2741	438	92.92	7.08	13.1158
Ambient pH	41362	2502	558	93.11	6.89	13.5170
Ambient pH	53935	1198	403	97.12	2.88	33.6883
Low pH	44380	1829	483	95.05	4.95	19.1955
Low pH	40352	2639	825	92.09	7.91	11.6490
Low pH	49857	1961	484	95.33	4.67	20.3914
Low pH	44940	1968	502	94.79	5.21	18.1943

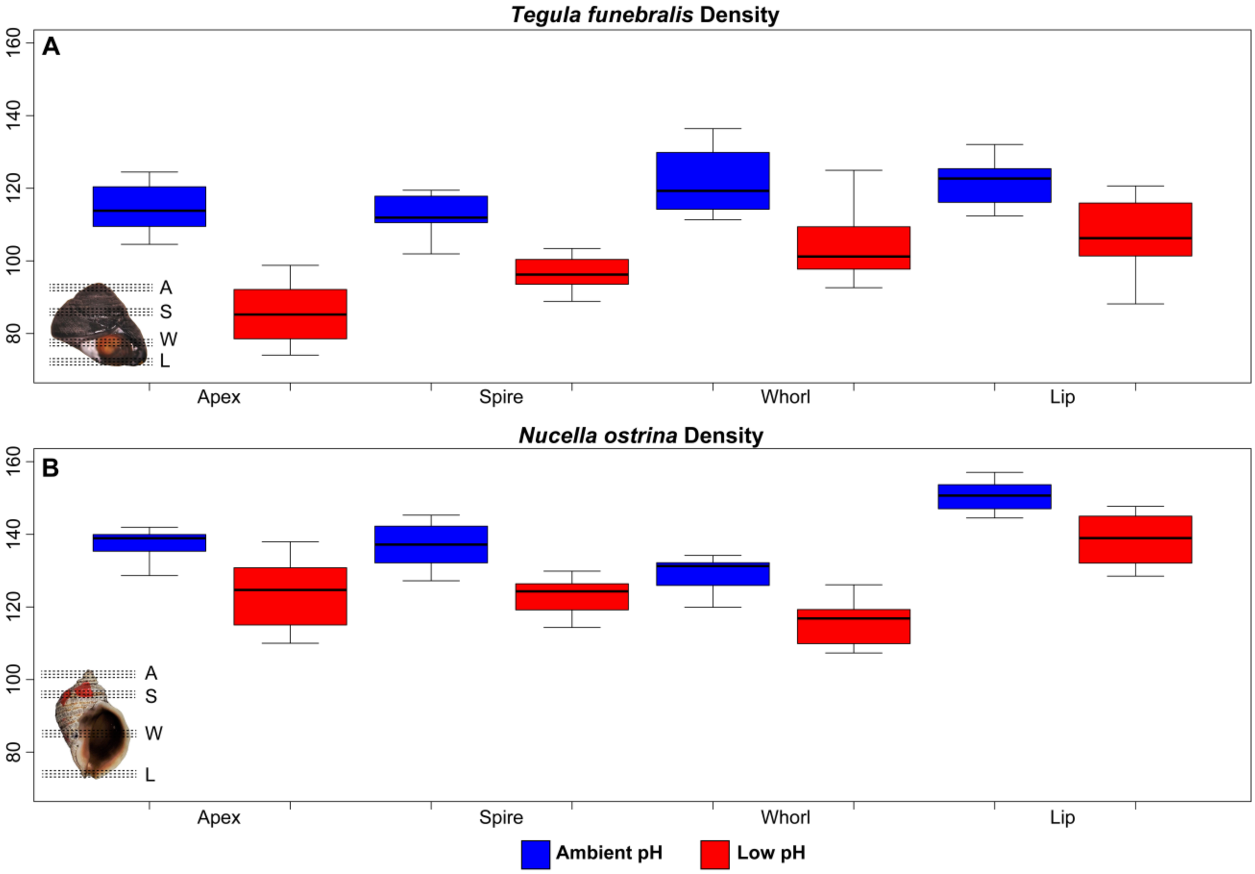

Figure 3.1

Density box and whisker plots based on average greyscale values from reconstructed microCT images slices. **A.** *Tegula funebralis.* **B.** *Nucella ostrina.* Treatments are coloured blue (ambient) and red (low pH). Gastropod images in the bottom left corner of each panel represent where reconstructed images from each shell were taken (as indicated by the dotted lines). Slices were taken from four regions of each shell, the apex (A), spire (S), mid whorl (W), and lip (L), with three replicate slices from each region. A 15 pixel-wide band was then traced around the exterior edge of each shell. Greyscale values of 0 – 255 (white - black) were assigned to each pixel, with the average greyscale value representing density for each slice. Greater average greyscale values indicated greater densities. Boxes represent upper and lower quartiles, central lines indicate medians, and whiskers represent min/max data.

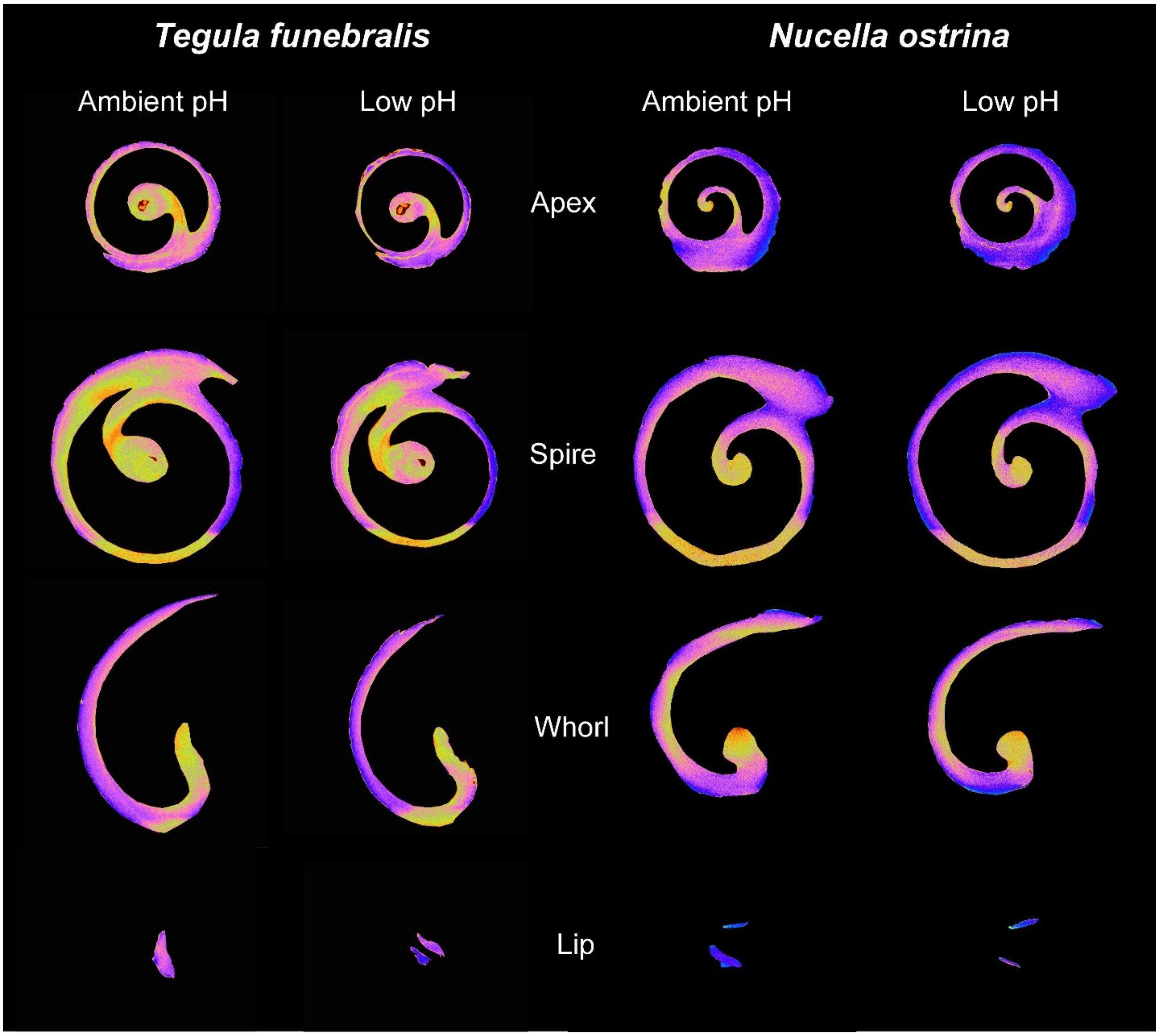

Figure 3.2

Representative reconstructed microCT images of *T. funebralis* and *N. ostrina*. The 16 bit “Color 2” module in DataViewer was applied, with cooler colours indicating areas of lower density. In *Tegula funebralis* (left columns), more jagged edges were visible on the external surfaces of the low pH specimens (second column) In spire images and whorl images in *T. funebralis*, the bottom of each image appears denser (warmer colours). This colouration was an artefact of the material that was used to mount specimens in the microCT scanner. For calculations of average greyscale values, the affected areas were cropped from the prepared image prior to analysis, and only the external edge of the shell (15 pixel-wide band) above that point was used to create the band of the shell surface.

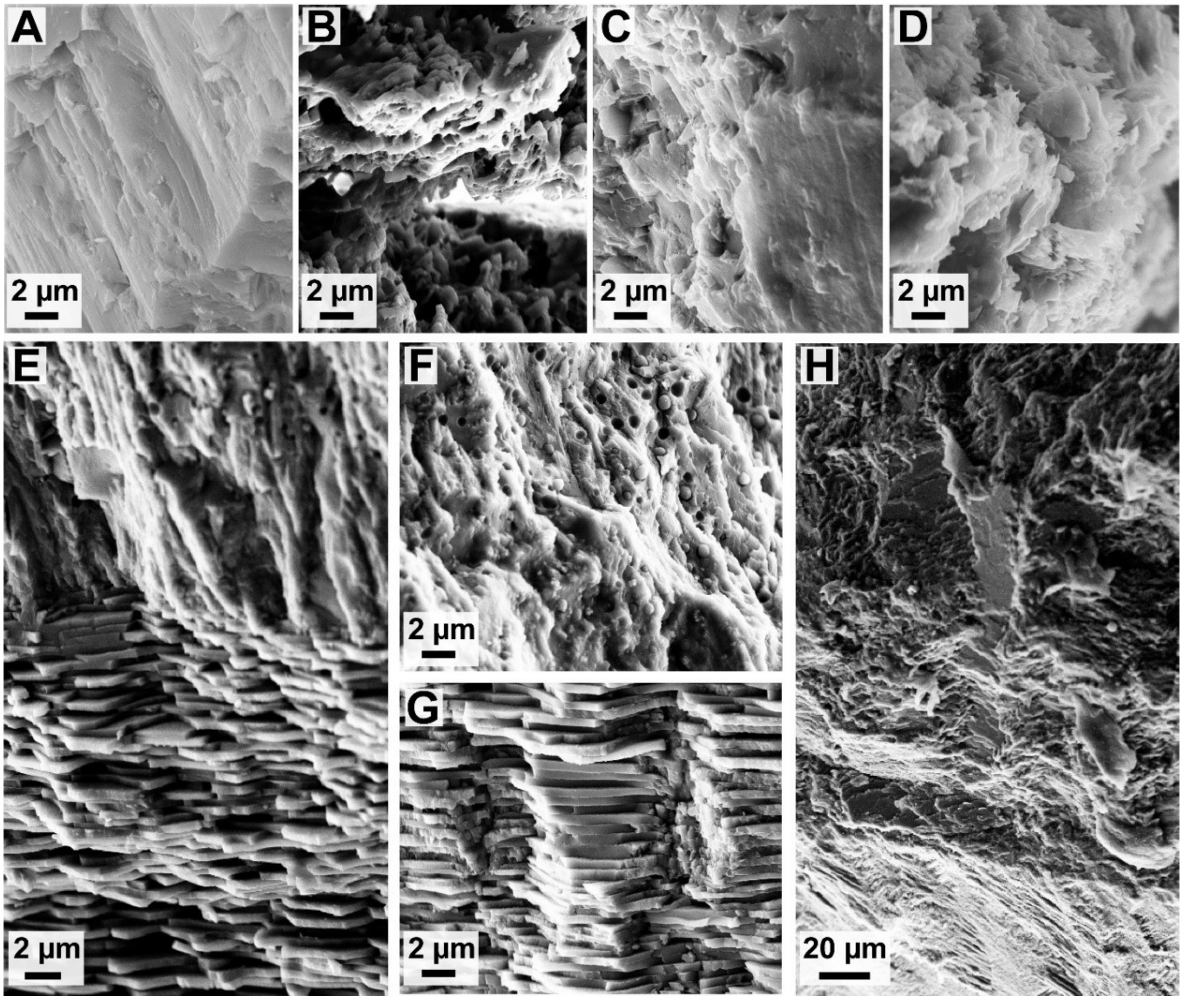

Figure 3.3

SEM images of shell microstructure in *T. funebralis* (A, B, E – G) and *N. ostrina* (C, D, H). Outer shell surface facing upwards all images. **A and B.** Shell surface of *T. funebralis* from ambient treatment and low pH treatments, respectively. **C and D.** Contrast of shell surface from ambient (C) and low pH (D) treatments of *N. ostrina*. Shell surfaces show rougher texture and pitting under low pH treatments (B and D). **E.** Transition from outer fibrous layer to inner nacreous layer of a low pH specimen, showing pitting into the fibrous layer. **F.** Circular pitting and "spheres" of a possible cyanophyte or prokaryote in the fibrous layer of *T. funebralis* from the low pH treatment, as described by Geller (1982*a*). **G.** Pitting and dissolution into the outer edge of the nacreous layer in *T. funebralis* from the low pH treatment. **H.** transition from external homogenous calcite layer to thin inner cross-lamellar layer in *N. ostrina*. Full cross section not shown, as homogenous layer was thicker than the field of view (~300 µm).

Chapter 4

Patterns of prey selection by the crab *Cancer productus* among three similar gastropod species (*Nucella* spp.)[2]

4.1 Introduction

Many predators, even generalists, often exhibit preferences for prey type (Murdoch 1969; Holt 1977; Vermeij 1977*b*; Creswell and McLay 1990; Boudreau and Worm 2012). However, the term "preference" implies active choice (Underwood et al. 2004), yet associations between predators and prey may depend on other factors, such as habitat or environmental conditions (Murdoch 1969; Menge 1976; Holt 1977; Menge and Sutherland 1987; Underwood et al. 2004). Crabs are important marine predators known to exert both direct and indirect control over their prey populations and distributions (Menge 1976; Bertness 1977; Boulding and Hay 1984; Menge and Sutherland 1987; Appleton and Palmer 1988; Palmer 1990; Marko and Palmer 1991; Behrens Yamada and Boulding 1996, 1998; Trussell et al. 2003; Bertness et al. 2004). Therefore, selection of prey by crabs can have important consequences for their prey and ecosystems. Along the northeastern Pacific, the red rock crab, *Cancer productus*, is a well known generalist predator in rocky intertidal habitats (Vermeij 1977*b*; Zipser and Vermeij 1978; Boulding and Hay 1984; Behrens Yamada and Boulding 1998; Grason and Miner 2012; Molinaro et al. 2014; Tyler et al. 2014, 2019; Stafford et al. 2015*a*; Behrens Yamada and Groth 2016; Mendonca et al. 2017) and its effects on the behaviour, morphology, and distribution of its prey have been well documented (Boulding 1984; Appleton and Palmer 1988; Palmer 1990; Marko and Palmer 1991; Behrens Yamada and Boulding 1996, 1998; Edgell and Neufeld 2008; Bourdeau 2009, 2010*a*, *b*, 2011,

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[2] This paper has been previously reviewed by the Journal of Experimental Marine Biology and Ecology. I have addressed all reviewer comments and resubmitted the paper as a new submission

2012, 2013; Edgell 2010; Mach and Bourdeau 2011). For example, there are three species of the gastropod genus *Nucella* in the Puget Sound region which exhibit varying levels of anti-predatory behaviour and induced morphological defenses when exposed to *C. productus* (Appleton and Palmer 1988; Palmer 1990; Marko and Palmer 1991; Edgell and Neufeld 2008; Bourdeau 2009, 2010*b*, *a*, 2011, 2012, 2013; Edgell 2010; Mach and Bourdeau 2011). However, it is unknown whether such morphological or behavioural defenses influence *C. productus* foraging behaviour or preferences, or whether *C. productus* is capable of distinguishing among these three closely related, and morphologically similar species. Here, we examine methods of foraging and prey selection among the three *Nucella* species by *C. productus*. The goals of the study were to determine any preferences or patterns of prey selection, as well as the potential causes for any observed patterns of predation, among similar, closely related prey.

Crabs have proven effective models for laboratory tests of foraging theory (Elner and Hughes 1978; Hughes and Seed 1981, 1995; Lawton and Hughes 1985; Ameyaw-Akumfi and Hughes 1987; Creswell and McLay 1990; Juanes and Hartwick 1990; Juanes 1992; Seed and Hughes 1995; Smith et al. 1999; Smallegange et al. 2008; Tyler et al. 2014). The majority of research thus far has demonstrated that while crabs usually select the prey item which improves “profitability” (Elner and Hughes 1978; Creswell and McLay 1990), crabs have been repeatedly shown to prefer smaller prey than would be predicted by foraging theory (Hughes and Seed 1981; Johannesson 1986; Ameyaw-Akumfi and Hughes 1987; Juanes and Hartwick 1990; Juanes 1992; Seed and Hughes 1995; Behrens Yamada and Boulding 1998; Smallegange et al. 2008). Most tests of crab prey selection have therefore focused on size ranges of prey taken by crabs (Elner and Hughes 1978; Bertness and Cunningham 1981; Hughes and Seed 1981, 1995;

Johannesson 1986; Ameyaw-Akumfi and Hughes 1987; Behrens Yamada and Boulding 1998; Smallegange et al. 2008), and it is generally concluded that crabs are more likely to consume smaller prey so as to avoid damage to their chelae (Juanes and Hartwick 1990; Juanes 1992; Seed and Hughes 1995).

Those studies which have compared different prey species have mostly focused on widely different species, such as mobile versus sedentary prey (Hughes and Seed 1995), native versus invasive species (Dudas et al. 2005; Grason and Miner 2012), prey that have different shell thicknesses or sculpture (Vermeij 1976; Bertness and Cunningham 1981; Lawton and Hughes 1985; Tyler et al. 2014), or prey that differentially burrow (Smith et al. 1999; Dudas et al. 2005). For example, crabs hunting infaunal bivalves tend to consume the first prey they encounter, regardless of size or profitability (Seed and Hughes 1995), yet are often less successful as burial depth increases (Smith et al. 1999; Dudas et al. 2005). Strategies also appear to be different when crabs are using visual versus tactile foraging (Hughes and Seed 1995).

It is also unknown how effective crabs are at differentiating among similar prey types, or if they select between "patches" of food, rather than simply among individuals (Macarthur and Pianka 1966; Stephens and Krebs 1986; Seed and Hughes 1995). For example, crabs often consume an entire clump of mussels, including small individuals that would not be considered profitable (Lin, 1991; Leighton and Tyler, in review). The following study examines crab prey selection within a "patch" of three similar species of the gastropod genus *Nucella* to examine influences on prey selection.

Along the Pacific northeast coast, there are three common species of the dogwhelk *Nucella* (*N. ostrina*, *N. canaliculata*, and *N. lamellosa*) that are frequent prey of the red rock crab, *Cancer productus* (Zipser and Vermeij 1978; Palmer 1985, 1990; Appleton and Palmer 1988; Marko and Palmer 1991; Edgell and Neufeld 2008; Bourdeau 2009, 2010*b*, *a*, 2011, 2012, 2013; Edgell 2010). *N. ostrina*, the purple dogwhelk, is the smallest of the three species (typically 1.5 – 2.5 cm in height), and while the intertidal range in which it lives overlaps with the other two species, its tidal range extends higher (Bertness 1977; Bourdeau 2011). *N. lamellosa* is the largest of the three species (typically 3 – 4 cm in height), and its tidal range extends lower than the other two species (Bertness 1977; Bourdeau 2011). All three species respond to the presence of *C. productus*, spending more time out of the water, reducing their foraging activities, and in some cases, manifesting induced defenses, such as morphological changes to the sculpture or thickness of their shell (Palmer 1985, 1990; Appleton and Palmer 1988; Marko and Palmer 1991; Edgell and Neufeld 2008; Bourdeau 2009, 2010*b*, *a*, 2011, 2012, 2013; Edgell 2010; Mach and Bourdeau 2011). However, the strength of such responses varies among species. *N. lamellosa* exhibits the strongest morphological changes; morphotypes from environments with little to no crab predation have multiple frilled lamellae, and thinner shells, whereas those from environments with greater rates of crab predation have smooth, thick shells, shorter spires, and large apertural teeth (Palmer 1985; Bourdeau 2010*b*, 2012). Some studies of *N. ostrina* have simply demonstrated reduced growth instead of induced morphological defenses in individuals exposed to predation cues (Bourdeau 2011). Shell thickening in *Nucella* has also been suggested to be a by-product of slower growth (Bourdeau 2010*b*).

Despite the numerous studies on the *Nucella*-*Cancer* system, there have been few studies which have focused on crab foraging behaviour and none on prey selection among species of *Nucella*. Given that *N. lamellosa* is the largest of the three species and is found lower in the intertidal zone, therefore spending more time potentially exposed to crabs who follow the tides to feed (Bertness and Cunningham 1981; Robles et al. 1989; Seed and Hughes 1995; Behrens Yamada and Boulding 1996), it is conceivable that *C. productus* may prefer *N. lamellosa*. However, *N. lamellosa* also has the best defended shell, presumably evolving as an effective deterrent to crab predation (Palmer 1985), and as mentioned previously, crabs are known to avoid prey which may damage their chelae (Juanes and Hartwick 1990; Juanes 1992; Seed and Hughes 1995). Another possibility is that *C. productus* may not even be able to distinguish the gastropod species, and instead selects prey items by size or shell ornament rather than by species. A closer examination of prey selection and foraging behaviour of crabs is therefore essential in understanding the role of crab predation in the ecology of both predator and prey species.

Preference is usually defined as a behavioural trait of a consumer, where preference is used to imply an active choice between food items (Singer 2000). However, preference can also be used to explain broadly any non-random pattern of resource consumption not explained by resource abundance (Chesson 1978). It is generally assumed that the “preferred” prey item is either more palatable, easier to handle and consume, and/or provides more nutrition, therefore maximizing the “profitability” to the predator (Charnov 1976; Krebs 1977; Stephens and Krebs 1986). Examining preference/food selection can be complicated by how one defines or interprets “preference”, leading to disagreement on proposed study designs and analysis in the past (Manly et al. 1972; Manly 1993, 2006; Taplin 1997, 2007; Underwood and Clarke 2005, 2006, 2007; Jackson and Underwood 2007). One method used on crabs suggests a two stage experiment, wherein the predator is presented with only one food item at a time in Stage 1, and then provided with both food items simultaneously in Stage 2 (Underwood et al. 2004; Underwood and Clarke

2005; Jackson and Underwood 2007; Grason and Miner 2012). The predator is usually left with an abundance of prey for a given length of time, and the proportion of prey consumed at each stage is then determined (Underwood et al. 2004; Underwood and Clarke 2005). Any change in the proportions of either prey type consumed when presented alone versus simultaneously therefore indicates true behavioural "preference" for or against a prey item (Underwood et al. 2004; Underwood and Clarke 2005, 2006, 2007). However, the study design requires an abundance of prey items, such that the predator is unable to consume all of the prey items. Depending on the prey species, it may not always be possible to collect enough individuals without potentially putting population sizes and ecosystem balance at risk while still maintaining sufficient replicates to produce a robust study. Another simpler test for preference is to conduct only Stage 2, where the prey items are offered simultaneously, and rank the order in which prey items are consumed (Taplin 1997, 2007). It is then straightforward to compare the rank-orders between prey items. Order still implies a "preference" by the predator, even if the reason for the preference is not known (Taplin 2007), or perhaps not even a true choice.

While predators are well known to influence the biology of their prey, there is also potential for prey adaptations and behaviour to influence prey selection in predators. To improve our understanding of the variables which control predator preference, as well as the importance of crab feeding behaviour and prey selection, the following study seeks to determine: 1) any potential preferences *C. productus* may exhibit among three closely related species of gastropod (*Nucella* spp.), and 2) patterns of prey selection within a "patch" of similar prey. We then speculate on the possible causes driving observed crab preferences and patterns of selection among closely related prey.

4.2 Methods

4.2.1 Gastropods

Approximately 90 individuals each of *Nucella ostrina*, *N. canaliculata*, and *N. lamellosa* were collected from Deadman Bay, San Juan Island (48° 30' 44.7" N 123° 08' 40.9" W) in May, 2018, and brought back to Friday Harbor Laboratories. *N. ostrina*, the purple dogwhelk, was easily recognized by its size, as well as the purple interior of its shell (only observed in living animals) (Fig. 4.1A). *N. canaliculata*, the channelled dogwhelk, has distinctive, regular "channelled" shell sculpture, particularly when compared to *N. ostrina* (Fig. 4.1B). In addition to being larger, *N. lamellosa*, the frilled dogwhelk, has tan – white shell colouration (shell colouration and striping can be more variable in the other two species), with two end-member morphologies: a thick, low spired shell with apertural teeth and no shell ornament, and a thinner shelled morph with multiple frilly lamella. Thicker shelled morphs are associated with environments that have abundant crabs (Palmer 1985). *N. lamellosa* from Deadman Bay resembled the thick-shelled morphs, as they had thick shells with apertural teeth and no prominent frills (Figs. 4.1C, 4.2D). Each specimen was uniquely labelled using coloured nail polish on the apex and a numbered wire marker on the same relative position of the body whorl, and then measured (height and maximum width) using digital calipers (± 0.01 mm). Previous work has shown that such methods for labelling prey do not inhibit crab feeding (Mendonca et al. 2017). The gastropods collected were average-sized individuals for each species, (height = 20.76 mm ± 1.75 for *N. ostrina*, 24.92 mm ± 2.90 for *N. canaliculata*, and 32.09 mm ± 3.73 for *N. lamellosa*).

4.2.2 Crabs

Fourteen adult male *Cancer productus* (average maximum carapace width 143.59 mm ± 6.96) (Table 4.1) were caught from the foreshore docks at Friday Harbor Laboratories using drop nets baited with cat food. The crabs were placed in round tanks with bricks for them to hide against to help them acclimate to laboratory conditions. Once all crabs had been caught, they were each fed and then starved for seven days to equalize hunger among individuals. Crabs were labelled by placing a lettered wire marker on the right anterior side of the carapace. Maximum carapace width and claw height, both right and left (taken as the height of the propodus immediately behind the dactyl joint), were then measured for each crab (Table 4.1). After the starvation period, crabs were placed individually in a tank and presented with one crushed individual each of *Nucella ostrina*, *N. canaliculata*, and *N. lamellosa*, and left in the tank until they had consumed the snails to ensure equal familiarity with the experimental food items.

4.2.3 Trials

For each experimental feeding trial, three individuals of each gastropod species were selected and placed in a 3x3 grid pattern in the arena tank (1 x 1.5 m). Gastropod placement was semi-random in that the order was different for each trial, but each row and column of the 3x3 grid had one individual of each species, ensuring that crab “choice” for species would not be biased by a distribution in which two individuals of the same species were adjacent to one another. For each trial, the three individuals within each species were selected based on similarity in size to one another, but not between species, as the three species vary naturally in size. These sets were recorded ahead of time, and chosen for each trial by reaching into their tank and using the set of the first gastropod of each species pulled from their holding tanks.

Gastropods were placed approximately 10 cm apart. The position of each individual gastropod was also recorded. If the gastropods moved during the trial (less than one individual per trial on average), they were carefully repositioned using a small pole between crab feeding encounters so as not to disturb the crab. Crabs appeared unaffected by the water movement caused by the pole.

Each of the 14 crabs participated in two feeding trials, resulting in a total of 28 trials with 252 gastropods (84 of each species). The two sets of trials were conducted using the same order of individual crabs to ensure an equal level of hunger among crabs. Individual crabs were introduced to the arena tank by placing them at the rear of the tank. As *C. productus* is primarily a nocturnal forager (Robles et al. 1989), all trials were conducted under red light, allowing for clear observation of the crabs without disturbing their behaviour, as crabs cannot see well in the red spectrum (Cronin and Forward 1988). The position and order of snail consumption was recorded, with the order ranked from first (1) to last (9). Trials were not time-limited, but continued until the crabs had consumed all nine snails, which usually took approximately one hour. If a crab lost interest in feeding or no foraging/hunting behaviours were demonstrated, the trial was continued for another hour before it was ended, which only occurred in two trials, once where the crab abandoned the last snail after only 37 seconds, and once where the crab only consumed 6 of the 9 snails. In the second instance, the three unconsumed snails were “tied” for last, and all were given a rank of 9. Both handling and grappling time were also recorded for each encounter. If a crab was unable to kill a snail successfully, the attack was still ranked in the order in which it was selected, as this was still considered a “choice” by the crab (there were only three instances where this occurred (all *N. lamellosa*), and the crabs spent a minimum of nine minutes handling the snails before they were abandoned). Between each trial, the tanks were cleaned and drained to avoid any mixing of chemical effluents from the crabs, snails, or consumed snails between trials.

4.2.4 Analyses

To test if rank order of the prey items was influenced by either species or size, we conducted a series of ordered regression models, or cumulative link mixed models, with rank as our dependent (response) variable, species and size as fixed effects, and crab and trial as random effects. To determine if grappling or handling times were affected by either species or size, generalized mixed models (family = gamma(link=log)) were fit and tested as described above for the rank data. Model performance was ranked using Akaike Information Criterion (AIC) scores, with the lowest score indicating the best model. Performance of the models were also compared using log-likelihood comparison tests, first of the full model against a null model with no fixed effects, and then comparing the full model to a species-only and size-only model. The significance of the fixed effects for models was then further explored using Wald Z-test scores.

However, while multicollinearity does not affect model performance, if variables (such as species and size) show strong multicollinearity, interpretation of the coefficients can become difficult. We therefore tested for multicollinearity of species and size on the response variable prior to interpreting the significance of the fixed effects by running a partial correlation on the residuals of a species only and size only linear model. If multicollinearity is strong (e.g., variables have very similar effects on the response variable), proper interpretation of the effects and significance of the coefficients can be obtained by analyzing the multicollinear fixed effects in separate models, provided there is no significant difference in either model's performance.

Models were built and tested using the package “ordinal” for ranked data and “lme4” for encounter time data in R v 3.4.4.

In experiments where selection is ranked without replacement, the probability of selecting one species over another changes after each encounter. In statistics, this is known as an urn problem. For example, at the beginning of the experiment, there is an equal probability (3 of 9, or 33.3% chance) under a random model that a crab will select any of the three species of *Nucella* as its first choice. But if a crab were to consume an individual of *N. lamellosa* as its first “choice”, the random probabilities among the three species have now changed for the crab’s next encounter (3 of 8 or 37.5% chance for *N. ostrina* and *N. canaliculata*, but only 2 of 8 or 25% for *N. lamellosa*). To address this changing probability, hypergeometric distributions were applied to establish the random expectation/probability for selection of any prey item under any possible combinations of choices. The hypergeometric distribution categorizes each selection as either a “success”, or “failure”, and then determines the probability of *k* successes out of *n* selections, where the number of *K* objects in *N* sample size is known. In our study, the hypergeometric distributions were applied separately to each of the three species by coding each selection as “success” when the desired species was selected, or “failure” when either of the other two species was selected. For example, if we were to determine the probability of selecting *k N. lamellosa* (*L*) in *n* draws, the formula would be as follows:

$$P\ (L = k) = \frac{\binom{K}{k}\binom{N\,-\,K}{n\quad k}}{\binom{N}{n}}$$

where vertical terms within parentheses, e.g. $\binom{K}{k}$ are binomial coefficients. Therefore, the probability of selecting *N. lamellosa* as the first two prey would be:

$$P\ (L = 2) = \frac{\binom{3}{2}\binom{9}{2} - \binom{3}{2}}{\binom{9}{2}}$$

$$= \frac{\left(\frac{3!}{2!\,(3-2)!}\right) \times \left[\left(\frac{9!}{2!\,(9-2)!}\right) - \left(\frac{3!}{2!\,(3-2)!}\right)\right]}{\left(\frac{9!}{2!\,(9-2)!}\right)}$$

$$= 0.0833$$

Once the probabilities, or hypergeometric distributions, for all combinations of selections for each species was determined, a 2x2 chi-square test was conducted to compare the number of trials in which each combination was actually observed (for example, in how many trials were two *N. lamellosa* selected in the first three encounters vs. not?) to the number of trials in which each combination was expected (total number of trials * probability (*P*) of 2 *N. lamellosa* in the first 3 encounters vs. probability of any other combination). For the previous example, the chi – square table would appear as:

	Observed	Expected
# of trials where 2 *N. lamellosa* were selected in first 3 encounters	10	28 * 0.21 **=6.00**
# of trials where 2 *N. lamellosa* were NOT selected in the first 3 encounters	18	28-6.00 **=22.00**
Total number of trials	28	28

The results of the chi-square tests determined if our results generated any combinations in which any species was selected significantly more often than expected for a given number of encounters. For scenarios where the expected and/or observed values violated the sample size requirements for a chi-square test, a Yate’s correction was applied to the chi-square test.

Additional 2x2 chi-square tests were performed to determine if position of the gastropods was important. The chi-square tests determined if crabs attacked a) the corner gastropods, b) the row of gastropods closest to the starting position of the crab, c) edge gastropods, or d) gastropods adjacent to the previously selected gastropod more than expected by random chance. All chi-square tests were conducted in Excel.

4.3 Results

Crabs attacked all but three gastropods, and only abandoned four individuals (3 *N. lamellosa* that the crabs could not crush, and one *N. canaliculata* which the crab abandoned quickly and then became focused on escape rather than feeding. Both species and size significantly affected rank of selected prey, although the effects of either variable were indistinguishable (model performance was the same whether both or only one was included) (Table 4.2). Species and size showed strong multicollinearity (partial R = 0.9937, $p < 0.0001$), suggesting that they both had the same effect on rank, presumably because the primary difference between species was size. We therefore interpreted the significance of species and size separately, with both indicating the same result. Crabs selected for *Nucella lamellosa* over both other species of *Nucella* (Table 4.2). There was no significant difference in selection between *N. ostrina* or *N. canaliculata* (Table 4.2), indicating that crabs only favoured *N. lamellosa* and did not, or could not, distinguish between the *N. ostrina* or *N. canaliculata*. Larger gastropods were also more highly ranked (Table 4.2). However, the AIC score for the model including size was slightly lower than the score for the model including species, even though the model performance was not significantly different between the models. For models of grappling and handling times, size was a better predictor than species (Table 4.2), although the performance of the size-only models was indistinguishable from the full model, and species and size again showed strong multicollinearity (partial $R > 0.96$, $p < 0.0001$), so the effects of species and size were analyzed separately.

Chi-square tests of the hypergeometric distributions conducted on *N. lamellosa* versus both other species indicated that all three individuals of *N. lamellosa* were selected significantly more than expected in the first seven encounters ($p = 0.041$) (Table 4.3). There were no trials in which neither of the last two gastropods were *N. ostrina* and/or *N. canaliculata* (11 trials with one of two, and 17 trials with both). While not significant, in many cases it was observed that one *N. lamellosa* was selected in both the first, as well as the first two encounters ($p = 0.061$, and 0.059 respectively) (Table 4.3). There were only five trials in which *N. lamellosa* was not selected in the first two encounters, and two trials in which it was not one of the first three selected (compared to 15 and 10 for *N. ostrina*, and 12 and 5 for *N. canaliculata*). However, all other combinations of draws, such as three *N. lamellosa* in the first six encounters ($p = 0.301$), were not significant (Table 4.3).

Crabs attacked corner gastropods first in 22 of 28 trials, which was significantly more than expected ($p < 0.001$) (Fig. 4.3). For both the second and third encounters in each trial, crabs were also more likely than expected to attack an adjacent gastropod to the one just previously attacked ($p = 0.001$ and 0.007 respectively) (Fig. 4.3). However, crabs did not favour the back row or edges on the first encounter more than expected ($p = 0.142$ and 0.204 respectively).

4.3.1 Observations

Once crabs acclimated to tank conditions, they exhibited typical hunting/foraging behaviours, where they would sweep the walking legs out, then towards the abdomen, and stretch the claws forward, occasionally scooping or bringing the claws to the mouth (Fig. 4.2B, C). In the trial where the crab only consumed 6 of the 9 snails, it eventually stopped displaying these hunting behaviours and instead became intent on investigating and attempting to climb the walls of the tank. We assumed that the primary means of prey detection were chemical and/or tactile, but may have also been facilitated by vision. As we could not directly test chemical effluents because crabs were exposed to a potential mix of all three gastropods at the same time, we mostly limit our observations to tactile responses of the crabs, but recognize that general detection may also have been facilitated by visual and chemical cues from the three gastropods. Minimally, crabs likely initiated hunting behaviours in response to chemical signals from the gastropods, as they exhibited hunting behaviours prior to encountering gastropods in each trial. We use the term “detection” herein to imply tactile recognition of prey by the crabs, unless otherwise specified.

Crabs most often encountered a gastropod with a walking leg. If the crab decided this walking leg encounter indicated potential food, they would sweep their legs along the outline of the gastropod to investigate further, and then would quickly grab the snail by using a combination of the walking legs and claws to draw the gastropod underneath itself (Fig. 4.2B, C). It is important to note that once this behaviour of sweeping the legs along the outline of the shell was initiated, the crabs always proceeded to attack the gastropod. In other words, the crabs never appeared to reject a gastropod, regardless of size or species, once it was recognized tactilely. Crabs would however, brush their legs against *N. ostrina* and *N. canaliculata* on occasion without pausing, which we did not count as a recognized encounter. Once the crabs had tactilely detected prey, the crabs would then use the chelae and mouth to manipulate the gastropod into an ideal crushing position in one chelae and attempt a static crush of the shell (Zipser and Vermeij 1978; Bertness and Cunningham 1981). For all encounters with *N. ostrina*, the crab was successful on this first crush (or in one instance, a peel), and began consumption of tissue in an average of 18.52 seconds (Table 4.2).

If the crab was not successful on the first crush, it would then use both chelae to squeeze the shell (Zipser and Vermeij 1978; Bertness and Cunningham 1981). While the majority of *N. canaliculata* were also crushed during the initial attempt, any that were not crushed initially were then crushed easily during this second, more precise crush, and tissue consumption began at an average of 47.88 seconds (Table 4.2). *N. lamellosa* took more time to crush (Table 4.2), and the crab would often use its mouth and chelae to switch the position of the claws back and forth for this second method of crushing. In most instances, the crab would eventually rip off the spire of the *N. lamellosa* using this method (Fig. 4.2D), exposing the tissue even though the aperture was still usually intact (Zipser and Vermeij 1978), with tissue consumption starting after an average of 179.89 seconds (Table 4.2). For the largest *N. lamellosa*, a peeling method was sometimes attempted, wherein the crab would insert the dactyls into the aperture of the gastropod, and simultaneously twist and pry at the outer apertural lip in an attempt to chip off pieces of the aperture until the crab could reach gastropod tissue (Zipser and Vermeij 1978; Bertness and Cunningham 1981). Peeling methods took considerably longer than crushing methods (268.52 and 31.86 seconds, respectively), and were not always successful, with the crabs failing in 3 instances. Crabs did not abandon these 3 *N. lamellosa* readily, spending at least 3 minutes before setting the gastropod aside and resuming foraging behaviour.

Once tissue consumption began, crabs would often already begin to use their walking legs to search for additional prey, sweeping the legs out and scooping them towards the abdomen (Bertness and Cunningham 1981). When the crab had finished consuming a snail, it would stand higher on its walking legs and resume foraging behaviours. Occasionally, the crab would encounter a piece of gastropod shell from a previous kill and stop to investigate and pick through the pieces to ensure it had consumed all of the tissue. Most often, the crab would then tactilely detect an adjacent gastropod, thus beginning the next encounter.

4.4 Discussion

Crabs showed a preference for both *N. lamellosa* as well as larger gastropods, but as *N. lamellosa* was larger than the other two gastropods, we were not able to distinguish the effects of size versus species. While crabs selected for *N. lamellosa* over *N. canaliculata* and *N. ostrina*, we suggest that this observed “preference” is not necessarily an active choice by the crabs, but an artifact due to the improved ability to recognize larger prey tactilely. If we had expected crabs to select for prey species or size actively, we might have expected to see rejection of less favoured prey items, yet once a crab tactilely recognized potential prey, it always attacked, regardless of species or size. The only instances of rejection were in fact three *N. lamellosa* that the crabs did attack but could not successfully crush, and one instance where the crab abandoned a *N. canaliculata*, but quit hunting behaviours and became intent on escaping. In addition, if we expected selection to be based on maximizing profitability or food intake, we would have expected to see a preference for *N. canaliculata* over *N. ostrina* (assuming both increased size and consumption/handling time indicated more food). Instead, crabs were most likely to attack the first gastropod they encountered and tactilely detected as prey, and then adjacent gastropods, regardless of species, suggesting that they simply attacked the first prey item they recognized. We therefore suggest that while size and food profitability might be the most likely benefit or outcome of the observed "preference" for *N. lamellosa*, crabs may not be actively selecting between the three species of *Nucella*. Rather, a more conservative hypothesis is that crabs simply attack the first prey they recognize, with "preference" for *N. lamellosa* most likely a by-product of size and their inability to always recognize smaller prey.

Based on foraging theory, it is possible that the preference crabs demonstrated for *N. lamellosa* may be an active choice, even if only based on size and not a choice among species, as larger prey presumably provide more food. While it took crabs significantly longer to grapple *N. lamellosa* (based on size), in general, the crabs were still able to grapple (crush or peel) *N. lamellosa* shells within a relatively short timeframe (less than 3 minutes) (Table 4.2). *N. lamellosa* were larger and therefore provided more tissue, as it took the crabs significantly longer to consume (handle) *N. lamellosa* once they had broken into the shell (Table 4.2). It is therefore likely that *N. lamellosa* provided enough food as to be worth the longer grappling times. However, if we assume that prey choice is based on profitability, we would have expected to see a preference for *N. canaliculata* over *N. ostrina*, as *N. canaliculata* were larger, and presumably provided more food value (longer consumption/handling times) (Table 4.2). The lack of preference for *N. canaliculata* over *N. ostrina*, suggests that crabs might not have been able to differentiate between the two species, regardless of whether the distinction might have been based on size, chemical effluent, or some other factor.

While it is possible that crabs might have been able to distinguish *N. lamellosa* from the other two species, if crabs actively preferred *N. lamellosa* over the other two species either because they chemically recognized their preferred prey, or because the latter two species were too small or did not provide sufficient benefit, one would expect any observed preference to be much stronger. For example, the hypergeometric probabilities did not indicate that *N. lamellosa* were selected significantly more than expected until the 7th draw, at which point all three *N. lamellosa* had been selected. Instead, crabs often appeared simply to work their way through the "patch" of gastropods, attacking the first gastropod they detected tactilely, which was usually a corner, and then an adjacent gastropod, at least for the second and third encounter, continuing until all nine gastropods were consumed (Fig. 4.3). Crabs never actively rejected a gastropod, except in one instance where the crab appeared to lose interest or was satiated and abandoned the last gastropod (*N. canaliculata*) in the trial after less than a minute, and three instances where the crabs were not able to crush the shells of *N. lamellosa*. If crabs are most likely to attack the first gastropods they encounter, did not reject gastropods, and the placement of the three species of gastropods in the 3 x 3 grid was dispersed evenly (a model of the effect on relative position performed no better than a null model), the apparent preference for *N. lamellosa* is unlikely due to active choice.

Alternatively, we suggest that it is more conservative to assume that rather than actively choosing *N. lamellosa*, crabs attack the first gastropod they tactilely detect, and are simply more likely to recognize and attack *N. lamellosa*. For example, several times in each trial, the crabs would brush against a smaller gastropod, usually *N. ostrina*, but often also *N. canaliculata*, and continue to forage without any interruption, as though they did not recognize that they had encountered a prey item. In contrast, *N. lamellosa* was always recognized whenever the crab encountered an individual. As mentioned previously, it was obvious when a crab tactilely detected potential prey because it would pause suddenly to investigate the outline of the “object” with its walking legs, and then would quickly grab the prey item. When the crab was down to the last 2 snails, which always included at least one of the smaller species (1 of 2 in 11 trials and 2 of 2 in 17 trials), it would take the crab much longer to find and attack the snails, even if it had encountered them with walking legs. The crab almost had to encounter the last 2 snails with more than one walking leg before becoming aware that it might have encountered potential prey and demonstrated the typical behaviour of using the walking legs to investigate the outline of the snail. The crabs’ difficulty in tactilely detecting the smaller species is also emphasized by the result that crabs were more likely to attack all three *N. lamellosa* in the first seven encounters (p = 0.041) (Table 4.3).

Selection for *N. lamellosa* and/or ideally sized prey may therefore not necessarily imply active choice by the predator. Species and/or size selection may simply be a by-product of either the predator’s ability to detect prey tactilely, and/or the predator’s familiarity or experience with prey that fall within its natural prey size range. As crabs are primarily nocturnal foragers (Robles et al. 1989) and rely on both chemical and tactile methods of foraging over visual (Elner and Hughes 1978), but see (Hughes and Seed 1995), it seems plausible that smaller prey are more likely to go undetected, or mistaken for something other than food (i.e., substrate). While the crabs in our experiment did demonstrate chemosensitivity to the gastropods, as they would initiate foraging activity (i.e. sweeping the walking legs and chelae in search of prey shortly after being placed in the tank), the precision of this chemical detection remains untested. Further tests of chemical detection could include a Y-maze experiment to see if crabs respond differently to each species' effluent. However, crabs appeared to initiate tactile hunting behaviours, even if they were not travelling in the correct direction, suggesting at least some reliance on tactile hunting strategies. Such tactile detection and foraging behaviour is also demonstrated by crabs that attack infaunal prey, and are also more likely to pursue the first prey they encounter (Smith et al. 1999; Dudas et al. 2005).

Interestingly, the antipredatory strategies of the gastropods appear to support general detection/recognition as the crab's primary method of prey selection, regardless of whether detection is chemical, visual, or tactile. For example, as we also observed during the trials, *N. ostrina* are known to place their apertures flush with the substrate when a crab is chemically detected, and in general either avoid movement, or seek refuge in a crevice or under rocks if available (Mach and Bourdeau 2011). In contrast, many other gastropods, such as *Tegula funebralis*, are much more active when exposed to the scent of a crab, and often attempt to leave the water (Jacobsen and Stabell 2004; Mendonca et al. 2017). Presumably, firm attachment of the aperture would increase attachment strength, as well as reduce bodily effluent used by chemosensitive predators such as crabs. In the case of our experiments, it was common for *N. ostrina* to position their apertures flush with the substrate, and few moved throughout any of the trials. Individuals of *N. lamellosa* and *N. canaliculata* were more mobile during the trials, although we only had to reposition approximately one individual per trial. Some crustaceans, such as lobsters, are also known to respond visually to more mobile prey (Hirtle and Mann

1978). As well, *N. ostrina* has shown greater reduction in its absolute foraging rates (Bourdeau 2013), and less shell growth (Bourdeau 2011) in response to predation cues than the other two species of *Nucella*. Such strategies would align with our conclusion that crabs select prey based on detection, both tactile and possibly visual and/or chemical: small, unmoving gastropods which minimize their chemical effluent and movement might impede the ability of the crab to detect the gastropod. Avoiding general detection is likely more critical for *N. ostrina* that have smaller, more vulnerable shells, and weaker induced defenses, than their larger congenerics (Bourdeau 2011, 2013).

Whether "preference" for *N. lamellosa* is due to active choice, chemical or tactile recognition, or some combination of factors, the observed selection of *N. lamellosa* over both other species still has important ecological implications. As mentioned previously, all three *Nucella* live at different, but overlapping, heights within the tidal zone, with *N. ostrina* occurring highest and *N. lamellosa* occurring lowest (Bertness 1977; Bourdeau 2011). Gastropods found lower in the intertidal zone spend more time exposed to crabs (Bertness and Cunningham 1981; Robles et al. 1989; Seed and Hughes 1995; Behrens Yamada and Boulding 1996). Detection, or lack thereof, is therefore probably critical for the mid-tidal range *N. canaliculata*, which takes no more time to crush or consume than the smaller *N. ostrina*. Indeed, despite the larger, more well defended shells of *N. lamellosa* which took longer for crabs to grapple (Table 4.2), crabs were still able to consume *N. lamellosa* with relative ease, most often entering the gastropod by ripping the spire off and rendering the apertural teeth useless as a defense (Fig. 4.2D). While there were only three instances where the crabs were unable to crush individuals of *N. lamellosa*, all three individuals were large. The larger size range in *N. lamellosa* is therefore probably just as important as induced apertural teeth/defenses (e.g., Whitenack and Herbert 2015). Given that *N. lamellosa* live lower in the intertidal where they are more regularly exposed to crabs, large body size is likely a strong selective pressure for *N. lamellosa*. *N. ostrina* and *N. canaliculata* most likely rely on the reduced likelihood of encounters given their higher tidal range, and when exposed to crabs during higher tides (Behrens Yamada and Boulding 1996), would be reliant on the crab's inability to recognize smaller prey.

Regardless of species preferences, chemical, or tactile recognition, our results indicate that crabs are most likely to attack the first gastropod they detect. Minimally, this suggests that crabs are not likely to reject food within a patch once they have encountered a first prey item, even if it is not the most profitable food item. "Preference" is often anthropomorphized to assume active choice on the part of the consumer. While *Cancer productus* also selects for *N. lamellosa*, we conservatively suggest that this "preference" is a consequence of crabs having difficulty recognizing smaller *Nucella* as potential prey. If the crab actively preferred *N. lamellosa*, we would expect at least some rejection of the smaller two species of gastropods. Instead, we find that crabs are more likely to attack the first gastropod they recognize, and sometimes simply do not realize they have encountered a smaller gastropod.

Our results lay the groundwork for further tests of crab selection among these gastropod species. For example, to test for a true preference of *N. lamellosa*, we suggest an additional replicate experiment be conducted in which gastropod size is controlled, which was not possible for this experiment given logistical constraints and lack of abundant small *N. lamellosa* near the chosen field site. However, it is likely more conservative to assume that crabs prefer larger gastropods, which naturally includes the larger *N. lamellosa*, simply because it is easier for crabs to detect larger prey tactilely over the smaller *N. ostrina* or *N. canaliculata*. We therefore conclude that crabs are most likely to attack the first gastropod they tactilely detect in every encounter, with “preference” for larger species possibly being a passive by-product of prey recognition.

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Table 4.1

Size measurements for specimens in *Cancer productus* used in feeding trials. All crabs were male. Carapace width measurements were taken as the maximum width (distance between the tips of the second most posterior lateral spines). Claw/chela height measurements were taken as the maximum height of the propodus immediately proximal to the dactyl joint. Note that there is no crab L, as this specimen was rejected for use in feeding trials after the crabs had been labelled.

Crab ID	Carapace width (mm)	Right claw height (mm)	Left claw height (mm)
A	146.43	39.60	39.21
B	147.93	37.40	38.08
C	135.58	35.37	35.56
D	144.33	40.12	39.75
E	152.66	41.80	39.86
F	152.09	39.13	39.56
G	140.43	35.56	37.19
H	134.05	36.44	35.13
I	138.84	36.28	36.63
J	139.11	37.76	36.65
K	139.68	36.18	35.03
M	149.04	37.45	38.49
N	156.00	39.37	40.05
O	134.14	33.91	33.84
Average	**143.59**	**37.60**	**37.50**
SD	**6.96**	**2.09**	**2.00**

Table 4.2

Mixed model results and summary data for size (mm), and grappling and handling times (s). Cumulative link (ordered) mixed models were used for crab preference (rank) data. Generalized linear mixed models were used for grapping and handling times. Fixed effects were species and/or size, with individual crabs and trial as random effects. Model performance was compared by log-likelihood ratio tests ("vs." indicates which models were compared), with best models indicated by lower AIC scores. Fixed effects were assessed using Wald Z-test scores.

Cumulative link mixed models of rank (family = ordinal)

Model Name	**no. parameters**	**AIC**	**logLik**	**LR Stat.**	**df**	**Pr(>Chi)**	**vs.**
Null	10	1127.2	-553.6				
Full (species and size)	13	1122.8	-548.4	10.442	3	**0.0152**	vs. Null
Species only	12	1121.5	-548.7	0.7525	1	0.3888	vs. Full
Size only	11	1119.7	-548.8	0.9205	2	0.6311	vs. Full

	Random effects	**Name**	**Variance**	**Std. Dev**
(from full model)	**Crab**	(Intercept)	0	0
(from full model)	**Trial**	(Intercept)	0	0

Fixed effects	**Estimate**	**Std. Error**	**z value**	**Pr (>|z|)**
Height	-0.0634	0.0208	-3.0490	**0.0023**
N. lamellosa* vs *N. canaliculata	0.6390	0.2732	2.3390	**0.0194**
N. lamellosa* vs *N. ostrina	0.7979	0.2715	2.9380	**0.0033**
N. canaliculata* vs *N. ostrina	0.1589	0.2693	0.5900	0.5550

Grappling time (s) (family = Gamma (link = log))

Model Name	**AIC**	**BIC**	**logLik**	**Resid. Df**	**Resid. Dev**	**Chisq**	**Chi DF**	**Pr(>Chi)**	**vs.**
Null	2508.0	2522.0	-1250.0	241	2500.0				
Full (species and size)	2341.2	2365.7	-1163.6	238	2327.2	172.770	3	**<0.0001**	Null
Species only	2364.0	2385.0	-1176.0	239	2352.0	224.792	1	**<0.0001**	Full
Size only	2340.1	2357.7	-1165.1	240	2330.1	2.925	2	0.2317	Full

	Random effects	**Name**	**Variance**	**Std. Dev**
(from full model)	**Crab**	**(Intercept)**	0.0803	0.2834
(from full model)	**Trial**	**(Intercept)**	0.3067	0.5538
(from full model)	**Residual**		0.7631	0.8736

Fixed effects	**Estimate**	**Std. Error**	**t value**	**Pr (>|z|)**
Height	0.1508	0.0103	14.604	**<0.0001**
N. lamellosa* vs *N. canaliculata	-1.1223	0.1309	-8.575	**<0.0001**
N. lamellosa* vs *N. ostrina	-1.7451	0.1325	-13.168	**<0.0001**
N. canaliculata* vs *N. ostrina	-0.6229	0.1242	-5.015	**<0.0001**

Handling time (s) (family = Gamma (link = log))

Null	3129.3	3143.4	-1560.7	245	3121.3				
Full (species and size)	2920.4	2945.0	-1453.2	242	2960.4	214.970	3	**<0.0001**	Null
Species only	2944.6	2965.7	-1466.3	243	232.6	26.211	1	**<0.0001**	Full
Size only	2922.0	2939.6	-1456.0	244	2912.0	5.658	2	0.0591	Full

	Random effects	**Name**	**Variance**	**Std. Dev**
(from full model)	**Crab**	**(Intercept)**	0.0154	0.1242
(from full model)	**Trial**	**(Intercept)**	0.1128	0.3358
(from full model)	**Residual**		0.3230	0.5683

Fixed effects	**Estimate**	**Std. Error**	**t value**	**Pr (>|z|)**
Height	0.1079	0.0063	17.250	**<0.0001**
N. lamellosa* vs *N. canaliculata	-0.7894	0.0835	-9.825	**<0.0001**
N. lamellosa* vs *N. ostrina	-1.2988	0.0805	-16.135	**<0.0001**
N. canaliculata* vs *N. ostrina	-0.5093	0.0788	-6.460	**<0.0001**

Summary Data (mean ± SD)

	N. ostrina	***N. canaliculata***	***N. lamellosa***
Height (mm)	20.76 ± 1.75	24.92 ± 2.90	32.09 ± 3.74
Width (mm)	13.01 ± 1.07	14.21 ± 1.82	18.41 ± 1.97
Grappling time (s)	18.52 ± 15.56	47.88 ± 91.76	179.89 ± 302.02
Handling time (s)	92.43 ± 38.70	177.77 ± 192.65	432.73 ± 486.82

Table 4.3

Hypergeometric probabilities for all combinations of prey selection, and resulting p-values of 2 x 2 Chi-square tests. Significant p-values are in bold. Expected trials numbers are based on the proportion of 28 trials (the total number of trials conducted) calculated from the hypergeometric probability in the second column. Observed values are the number of trials in which the draw combination condition was met.

		Expected	**Observed**			**Chi-square**			**Yate's correction**		
Draws	**Hyp. Prob.**		*N. ostrina*	*N. canaliculata*	*N. lamellosa*	*N. ostrina*	*N. canaliculata*	*N. lamellosa*	*N. ostrina*	*N. canaliculata*	*N. lamellosa*
1 in 1	0.33	9.33	6	8	14	0.181	0.593	0.061			
1 in 2	0.5	14	13	16	19	0.705	0.45	0.059			
1 in 3	0.54	15	16	20	15	0.705	0.058	1			
1 in 4	0.48	13.33	16	17	12	0.313	0.165	0.614			
1 in 5	0.36	10	9	13	9	0.693	0.237	0.693			
1 in 6	0.21	6	8	5	2	0.357	0.645	0.065			
1 in 7	0.08	2.33	3	2	0	0.649	0.82	0.111	0.907	0.907	0.211
2 in 2	0.08	2.33	0	0	4	0.111	0.111	0.254	0.211	0.211	0.423
2 in 3	0.21	6	2	3	10	0.065	0.167	0.065			
2 in 4	0.36	10	7	9	13	0.237	0.693	0.237			
2 in 5	0.48	13.33	14	14	13	0.801	0.801	0.9			
2 in 6	0.54	15	14	20	17	0.705	0.058	0.449			
2 in 7	0.5	14	17	16	11	0.257	0.45	0.257			
2 in 8	0.33	9.33	9	13	5	0.894	0.142	0.082			
3 in 3	0.01	0.33	0	0	1	0.561	0.561	0.245	0.766	0.766	0.766
3 in 4	0.05	1.33	0	0	3	0.237	0.237	0.139	0.461	0.461	0.299
3 in 5	0.12	3.33	2	1	6	0.437	0.173	0.12	0.628	0.285	0.205
3 in 6	0.24	6.67	5	3	9	0.46	0.104	0.301			
3 in 7	0.42	11.67	7	9	17	0.074	0.307	**0.041**			
3 in 8	0.67	18.67	18	14	22	0.789	0.061	0.181			

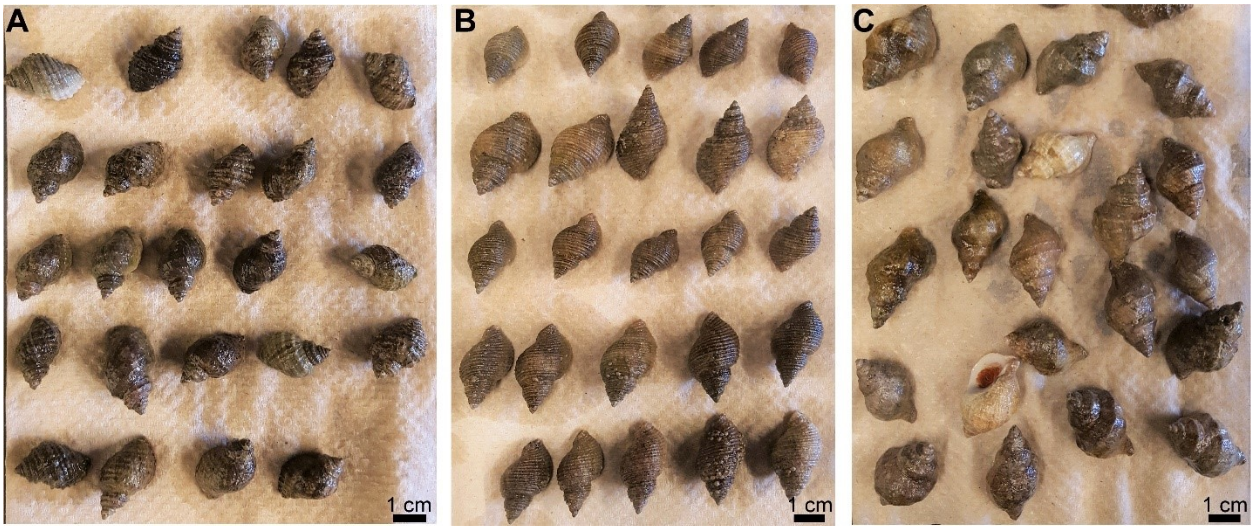

Figure 4.1

Images of the snails used for crab feeding trials. A. *Nucella ostrina.* **B.** *N. canaliculata.* **C.** *N. lamellosa*. All specimens were collected from Deadman Bay on San Juan Island in early May 2018. Scale bar (bottom right corner of panels) = 1 cm.

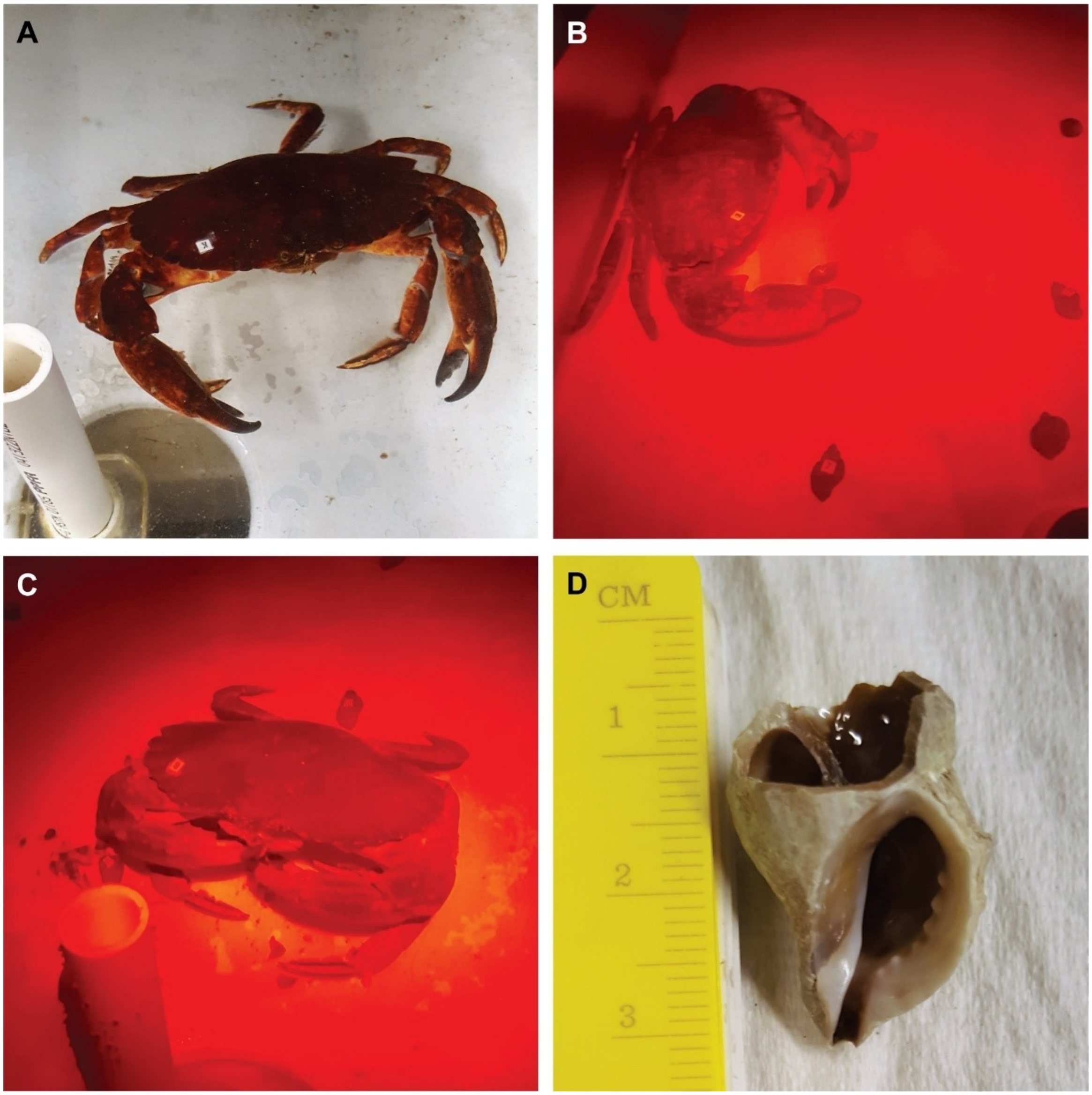

Figure 4.2

Images from crab feeding trials. A. Picture of Crab K in normal light prior to trial. **B.** Crab E demonstrating typical foraging behaviour and tactile detection of a gastropod (the crab has encountered the gastropod and has begun to position the chela to grab the gastropod). **C.** Typical feeding behaviour demonstrated by Crab G after a successful crushing attempt (note the front walking legs are sweeping shell pieces underneath the carapace). **D.** Typical shell damage to a specimen of *Nucella lamellosa* after a successful attack from a crab. Crabs most commonly entered the gastropod shell by ripping off the spire in a crushing attempt.

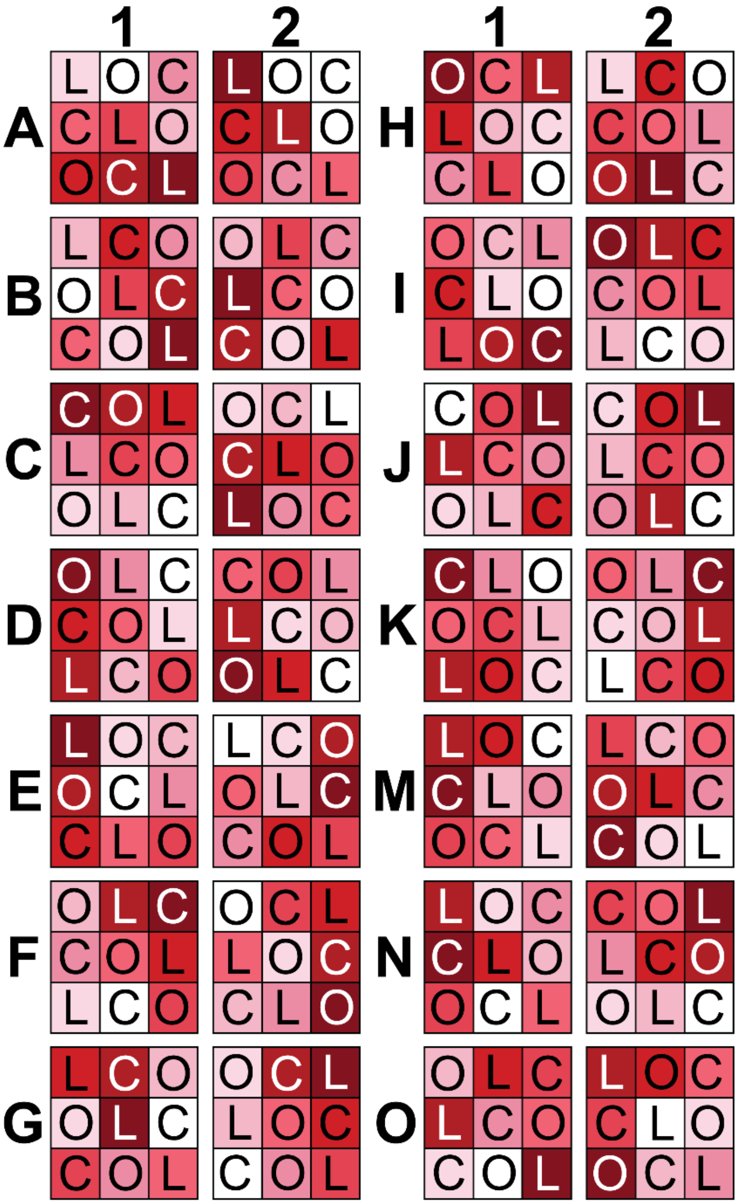

Figure 4.3

Position and rank order of gastropods in all 28 feeding trials. Each 3 x 3 grid represents the position of all gastropods for one feeding trial, with crab letter indicated to the right of the grids, and the trial number listed above. Letters in the grid indicate *Nucella* species (O = *N. ostrina*, C = *N. canaliculata*, and L = *N. lamellosa*). Colour indicates the rank order in which each gastropod was taken, with the darkest colour being the first, and white being the last/ninth.

Chapter 5

Regional variation drives patterns of crab predation on the gastropod *Tegula funebralis* along the west coast of Canada and the U.S.

5.1 Introduction

Evidence of predation in the form of scars left on prey provides a rich dataset in which to study patterns of predation both in modern and fossil ecosystems. In the fossil record, direct predation is impossible to observe, and predators often do not have the same preservation potential as their prey. Even in modern ecological studies, *in situ* predation studies require significant time and resources, especially when examining patterns across broad spatial/latitudinal scales. In marine systems, shell-crushing predators, such as crabs, leave distinct injury traces on their prey, known as repair scars. These repair scars have been used to examine predation over both evolutionary time scales (Vermeij et al. 1980, 1981; Schindel et al. 1982; Dietl and Alexander 1998; Dietl and Kelley 2002; Leighton 2002; Alexander and Dietl 2003; Dietl et al. 2010; Richards and Leighton 2012; Leighton et al. 2013; Mondal et al. 2014*a*; Mondal and Harries 2015), as well as environmental gradients (Cadée et al. 1997; Dietl and Alexander 2009; Molinaro et al. 2014; Harper and Peck 2016), and across recent environmental disturbances (Tyler et al. 2019). Along the west coast of North America today, direct evidence of crab predation is usually unknown, much like what is observed in fossil systems. Here, we used repair scars to explore potential patterns in modern crab predation on a common, widespread gastropod (*Tegula funebralis*) from Vancouver Island, British Columbia to San Diego, California. The goals of the study were to test for: 1) any broad-scale, regional, or local patterns in predation along a latitudinally extensive coastline, and 2) relationships between the frequency and size of attacks that could indicate whether variation in repair scars reflects predator abundance or success.

Unsuccessful predation is a common occurrence in most ecosystems, and is a necessary component for antipredatory selection in prey taxa (Vermeij 1982*a*). Durophagy (shell-crushing predation) has been a common method of predation since the Paleozoic (Vermeij et al. 1981; Alexander and Dietl 2003; Leighton 2011), in which evidence of failed predation is preserved in the form of repair scars with distorted growth lines on healed shells (e.g., Stafford et al. 2015*b*). Since the Mesozoic, crabs have become a major durophagous predator for molluscs, and are thought to be a major driver in the evolution of antipredatory forms in molluscs (Vermeij 1977*a*, 1983). On gastropods, repair scars from crabs are formed when a crab inserts its chela into the apertural opening and attempts to chip or "peel" back the aperture (Zipser and Vermeij 1978). These repair scars, sometimes also referred to as "peeling" traces, exhibit a consistent morphology attributed to the ichnogenus *Caedichnus* (Stafford et al. 2015*b*), identified by a wedge-shaped invagination of the whorl that cuts across growth lines (Fig. 5.1A).

There has been considerable work done examining repair scars in gastropods both in the modern ecological (Vermeij 1982*b*; Geller 1983; Schmidt 1989; Cadée et al. 1997; Dietl and Alexander 1998, 2009; Molinaro et al. 2014; Stafford et al. 2015*a*; Tyler et al. 2019) and palaeontological literature (Vermeij et al. 1981; Schindel et al. 1982; Alexander and Dietl 2003; Stafford and Leighton 2011; Leighton et al. 2013). The most common metric for assessing predation is to measure repair frequency, which is usually reported as the number or percentage of individuals in each sample that have a repair (Vermeij et al. 1980, 1981; Schindel et al. 1982; Vermeij 1982*b*, 1993; Geller 1983; Schmidt 1989; Dietl and Alexander 1998; Alexander and

Dietl 2001, 2003; Kowalewski 2002; Leighton 2002, 2011; Molinaro et al. 2014; Mondal et al. 2014*a*; Pruden et al. 2018; Tyler et al. 2019). However, interpreting changes in repair frequencies between samples is challenging, especially over broader temporal and spatial scales (Cadée et al. 1997; Mondal and Harries 2015), with concerns over whether a variation in repair frequency could be due to a change in predator success or the number of attacks (Vermeij 1987; Leighton 2002; Budd and Mann 2019). For instance, a decrease in repair frequency could indicate fewer attacks, but if the attack rate was held constant, the same result could be produced if crabs were more successful and failed less (with successful kills resulting in the destruction and removal of shell material). In the modern, studies of crab repairs on gastropods have found that repair frequency tracks crab attacks (Schindler et al. 1994), including studies of the prey gastropod *Tegula funebralis* (Molinaro et al. 2014; Stafford et al. 2015*a*). However, it is unknown whether patterns in repairs at this scale would be observed across a broader geographic range, or if relative predator success might also change over broader areas, such as a latitudinal gradient across a coastline. As patterns of success might shape broader evolutionary patterns between predators and prey, the ability to distinguish between predation pressure (the number of attacks) and predator success when examining trends in repairs across broad geographic or temporal scales is critical.

The size at which repairs occur can also be indicative of predator success (Alexander and Dietl 2001; Leighton 2002; Richards and Leighton 2012; Mondal et al. 2014*b*), but repair frequency by itself also does not shed any light on the size distributions of repairs, or any changes therein. Therefore, success might be more easily measured by shifts in the size at which repair scars occur (e.g., Alexander and Dietl 2001; Leighton 2002; Mondal et al. 2014*b*). As repair scars in gastropods are created via peels at the aperture, and gastropods grow by accretion, the placement of the scar also preserves the size at which the organism was attacked. The preservation of this spatial relationship between repairs and overall body size could not only provide a record of crab strength (and therefore success), but it would also potentially provide information on relative shifts in the size of repairs compared to overall prey size. For example, if the average size of repairs (size at attack) increased, it would indicate that crabs were stronger relative to the gastropods; not only were the crabs capable of attacking larger gastropods, but presumably stronger crabs would be more likely to successfully crush smaller gastropods, resulting in fewer repairs on smaller gastropods, as crushed individuals would be destroyed and removed (e.g., Pruden et al. 2018). Alternatively, if there was no change in the size of attacks, any observed differences in repairs would be most likely the result of a change in the number of attacks. Therefore, measures of the size of attacks could be used in conjunction with repair frequency to test the success of predators across broader spatial or temporal scales.

Variation in predation intensity and/or success might be caused by geographic variation in both predators and prey. For instance, latitudinal gradients in shell-crushing predation are thought to result in the greater diversity and evolution of gastropod antipredatory shell forms in the tropics compared to higher latitudes (Palmer 1979; Vermeij et al. 1980; Bertness and Cunningham 1981). Such latitudinal gradients in predation are known from other systems as well, such as drilling predation (Mondal et al. 2019), and both fossil (Leighton 1999) and modern brachiopods (Harper and Peck 2016). However, while patterns of diversity in species richness and body forms are commonly studied, latitudinal gradients of predation pressure or success against individual prey species are less well known.

Along extensive coastlines, predation may also differ due to variation in regional conditions, even if this variation does not form a latitudinal trend. The west coast of North America is typically separated into distinct regions that differ in oceanographic conditions, such as upwelling (Menge et al. 2004; Cooper and Shanks 2011). For example, the coast of Washington and Oregon experiences intermittent upwelling, whereas upwelling is more consistent and intense in northern California (Menge et al. 2004). Upwelling then becomes weak/relaxed in southern California (Menge et al. 2004). Past studies of predation between these regions have suggested that larval recruitment patterns of both predators and prey between upwelling regimes might influence the strength of biotic interactions (Sanford et al. 2003; Menge et al. 2004; Schemske et al. 2009). However, for those predators which have planktotrophic larval dispersal, such as crabs and sea stars, variation in predation rates may vary more with local conditions (Menge et al. 2004). Crab species' ranges and relative abundances may also be just as important. For example, the yellow rock crab *Metacarcinus anthonyi*, is only present in the southern part of California, and is smaller than some more widely distributed rock crabs, such as *Cancer productus* and *Romaleon antennarium*.

At a local scale, predation rates may be driven by a wide variety of factors, such as variation in microhabitat (Geller 1983; Schmidt 1989; Cadée et al. 1997), the density of prey (Menge et al. 2004), wave energy (Molinaro et al. 2014), and depth (Harper and Peck 2016). Changes in predation rates, as well as body shape/size of either predators or prey, may also just as easily be attributed to changes in temperature or multiple environmental conditions (Kroeker et al. 2016). The variation in repair rates at local scales can make it difficult to make inferences about broader patterns of predation, and it is therefore suggested that multiple sites within a region should be examined prior to drawing any conclusions on broad predation patterns (Cadée et al. 1997; Hoffmeister and Kowalewski 2001). Spatial and environmental variation in predation may also influence or obscure broader temporal or evolutionary trends in either predators or prey (Hoffmeister and Kowalewski 2001). Therefore, regardless of the cause of variation in predation, by examining repair scars in a single, morphologically conservative species at multiple sites within multiple regions along a coastline, it should be possible to establish a baseline of the possible spatial (regional, and/or latitudinal) patterns in predation. Once we discern any spatial patterns, we may test for underlying relationships, such as between repair frequency and size of attacks, which could potentially influence evolutionary trends.

The black turban snail, *Tegula funebralis* (Adams 1855) (formerly *Chlorostoma*), is a ubiquitous member of rocky intertidal communities along the west coast of North America. The species inhabits the mid to upper intertidal zone from about 0 – 2 feet above mean lower low water (MLLW) (Frank 1975). *T. funebralis* are common, if not preferred, prey for predators such as the sea star *Pisaster ocracheus* (Paine 1969*b*; Markowitz 1980; Fawcett 1984), and shell-crushing rock crabs like *Cancer productus* and *Romaleon antennarium* (Geller 1983; Stafford et al. 2015*a*). Latitudinal gradients in body size and population structure of *T. funebralis* have been noted in the U.S., with more, and larger, adults in Washington and Oregon compared to California, which breed at different times of the year (Frank 1975), and have different population structures (Frank 1975; Fawcett 1984; Cooper and Shanks 2011). Some studies have also suggested latitudinal gradients in the vertical distribution of *T. funebralis*, with predation restricting the depth of *T. funebralis* in southern California (Fawcett 1984). However, such effects appear to be restricted to smaller individuals, with the distribution of large adults being unaffected by predators (Markowitz 1980; Gravem and Morgan 2017).

Crab predation on *T. funebralis* has been well documented both in the lab (Geller 1982*b*; Mendonca et al. 2017), and in situ via repair scars (Molinaro et al. 2014; Stafford et al. 2015*a*; Tyler et al. 2019), but broad-scale geographic studies of crab predation on *T. funebralis* have not been explored. As with fossil studies that also lack information of the predators themselves, there is relatively little data for populations of adult rock crabs, such as *Cancer productus*, *Romaleon antennarium*, and *Metacarcinus anthonyi*, etc. along the west coast of Canada and the U.S. (Fitzgerald et al. 2018). At the provincial/state and federal level, rock crabs are of commercial interest as a fishery, but have been considered "least concern" and therefore have poor records, many of which did not differentiate species until as late as 1995 (Fitzgerald et al. 2018). As detailed information on the crabs themselves is lacking, a broadly distributed prey item, such as *T. funebralis*, can provide abundant data in which to test and examine trends in crab predation/repair scars over multiple geographic scales.

Here, we surveyed populations of *Tegula funebralis* for crab repair scars at 28 sites from four distinct regions of Canada and the U.S. (B.C., Oregon, northern California, and southern California) by measuring body size, repair frequency, and the size at which repair scars occurred. We then explored variation in each metric to determine if there were any potential broad-scale latitudinal, regional, or local patterns in predation. We also tested for any underlying relationships between repair frequency, snail body size, and the size of repairs, that could help indicate whether attack frequency or changes in success explained the observed patterns in predation. Such studies can be used to examine predator populations when access to information on the predators themselves is limited, and can also be used as a baseline for examining relationships between repair frequency and success across broader spatial and temporal scales.

5.2 Methods

5.2.1 Sampling Methods

T. funebralis surveys were conducted at 28 locations between Vancouver Island and southern California during the summer morning low tides between 2015 to 2019. The sites were from four distinct geographic regions: eight localities from British Columbia (near Bamfield, on Vancouver Island), eight from central – southern Oregon (between Depoe Bay and Cape Blanco), five from northern California (near Bodega Bay), and seven from southern California (four from the Palos Verdes Hills near Los Angeles, and three near San Diego) (Fig. 5.2). Within each of the four regions, we surveyed nearly all of the rocky intertidal coastline that was accessible, and sampled all of these sites that had *T. funebralis*, thereby capturing a representative range of local environmental conditions where *T. funebralis* is found.

More than 4,500 individuals of *T. funebralis* were surveyed for repair scars. Only adult *T. funebralis* (those having at least three body whorls) were included in the study, as smaller individuals are more likely to be successfully crushed by crabs and therefore experience little sub-lethal damage which would form a repair scar (*sensu* Molinaro et al. 2014). Furthermore, while the vertical distribution of smaller individuals (< three whorls) is potentially affected by predators (Markowitz 1980; Fawcett 1984), larger adults can be found throughout the full vertical range of *T. funebralis*, regardless of predators (Gravem and Morgan 2017). Collection of individuals was spread out as evenly as possible over the entire distribution of *T. funebralis* at each site to ensure there was no bias based on spatial or tidal position. Between 120 – 220 individuals were collected randomly from each study site (sample size varied depending on the length of time afforded by the tide cycle). Specimens were placed in buckets for collection. All measurements were taken *in situ*, with specimens returned to their approximate location once data collection was complete and before the tidewaters returned, to ensure minimal impact from the surveys. The entire process usually took two hours at each site.

Size measurements of each snail were taken using digital calipers (to 0.01 mm). For each individual, both maximum shell height and width were measured. As thickness measurements are prone to an unreliable level of error (Barclay, Leighton, unpublished data), and preliminary data showed no variation in shell thickness between sites (Stafford et al. 2015*a*, Barclay, unpublished data), thickness measurements were omitted for this study. Furthermore, *T. funebralis* is not known to have the strong variation in shell thickness or morphology observed in other gastropods, even with variation in predation pressure (Geller 1982*a*; Jacobsen and Stabell 2004; Barclay et al. 2019).

The presence or absence of repair scars, as well as the number of scars, was noted for each specimen. As peeling traces only occur at the aperture of the snail, and snails grow their shells by accretion, each repair scar essentially captures the size of the animal when it was attacked, including multiple attacks during its lifetime. Therefore, for each scar, a width measurement was taken denoting the size of the animal's shell at the time of the attack, referred to as size at attack (SAA). The shell was measured from the point at which the repair scar met the top of the whorl to the opposite side of the shell (passing through the apex/midpoint), as though the repair represented the leading edge of the shell, and thus measuring the width of the shell at the time of attack (Fig. 5.1B).

Comparisons of repair scar frequency between sites were conducted using two measurements from each of the 28 sites: 1) the proportion of individuals repaired (number of scarred individuals divided by the total number of individuals in the sample, reported as a percentage), and 2) the total repairs (total number of scars divided by the total number of individuals). Both measures are commonly used in repair scar studies (Leighton 2002; Alexander and Dietl 2003; Dietl and Kosloski 2013), often referred to as RF_1 and RF_2 "Repair frequency 1 and 2" (*sensu* Molinaro et al. 2014). Each method has strengths and weaknesses, as the proportion of individuals repaired (RF_1) does not capture individuals which are repaired more than once, while the percentage of total repairs (RF_2) can exceed 100% (if many individuals are repaired more than once). Here, we test RF_1 and RF_2 separately, but used the general term "RF" to infer general patterns of repair frequency when both metrics are in agreement.

5.2.2 Analyses

5.2.2.1 Regional Effects

We first examined potential differences between regions in the variables from each site (repair frequency, average gastropod size, and SAA), by running a series of Kruskal-Wallis (K-W) tests using Dunn tests with a Bonferroni correction for pairwise comparisons. K-W and Dunn tests were used as the non-parametric equivalent of a one-way ANOVA and Tukey HSD to account for violations of normality and homogeneity of variances due to unequal sample sizes between regions. These comparisons, along with box and whisker plots of the data, also indicated whether there were latitudinal patterns (i.e., did the differences proceed in a directional manner?). Given that RF_1 and RF_2 were both measures of repair, and height and width were both measures of size, we ran a Pearson's product moment correlation for each pair to test their agreement. As there was a strong correlation for both ($R >= 0.99$, 0.92, respectively), we only reported one of the measures for each (e.g., RF_1 and width) for conciseness, as the other variable would show the same results.

5.2.2.2 Influences on Repairs and Size at Attack

To determine if either the presence/number of scars, or repair frequency was also influenced by size or size at attack, we fit generalized linear regressions, with scars or RF as the dependent/response variable, and size and SAA as the independent variables. If the prior K-W tests indicated differences between regions, region was also included in the model as an independent variable. Separate models were conducted using data from the site (data aggregated at the site level, e.g., repair frequency) and individual levels (data collected from individuals, e.g., number of scars on an individual), as 1) the effects of size on the presence of a scar on an individual gastropod could be independent of the effects of overall gastropod size on repair frequency at each site, and 2) the dataset for individual SAA was independent of individual gastropods, as there could be multiple data points (repairs) from a single gastropod. For site-level models, average size and SAA from each site were used as the independent variables. For models of individual data, generalized mixed models were used (binomial family for scar presence/absence, and Poisson for scar count data), with size as an independent variable and locality as a random effect.

We also tested if SAA was influenced by size using a generalized linear model on site average data (SAA as the dependent variable, and size and region as independent variables).

Again, because the individual dataset for SAA was independent of size data collected from individual gastropods, we could not run a mixed model of SAA at the individual level because there were no comparable independent variables.

For each model, performance was assessed by conducting log-likelihood ratio tests comparing the model in question to a null (intercept-only) model, as well as using Akaike Information Criterion (AIC) scores, with lower scores indicating better models. Once we had determined the best model for each dependent variable, the significance of the independent variables (fixed effects) was examined using t-values and Wald-Z tests for generalized linear and mixed models, respectively. In cases where region and any independent variable were both found to have a significant effect on the response variable, we examined the strength and direction of the relationship between that independent variable and the response variable by running a partial correlation wherein we removed the effects of regional differences on the response variable. All analyses were performed in R (version 3.4.4) using the glm2 and lme4 packages.

5.2.2.3 Crab Strength/Relative Success

As mentioned previously, repair frequency may be a function of both the frequency of attacks, as well as the success of the predator at that site, which can make comparisons and interpretation of repair frequency between samples difficult. Size of attacks (SAA) was therefore used as a proxy for crab strength and success. For example, if SAA increased from one region to another, this suggests that crab strength increased, and repair frequency might therefore be impacted (we would expect RF to be lower because crabs were stronger and would have failed less often). However, if overall gastropod size also increased, RF might not be affected because the shift in success (SAA) might be relative to the shift in overall gastropod size. In other words, despite the increase in crab strength and loss of failures on smaller gastropods, there are now relatively more large gastropods to attack, so the overall observed number of repairs might not be different than the site with smaller gastropods and weaker crabs because the change in repairs is proportional. Therefore, in any sample, it is possible to use SAA to measure both crab strength, as well as the relative success of crabs against the gastropods available to them, particularly with regards to how repair frequency might be affected or compared between samples (Fig. 5.3). For example, an increase or decrease in crab strength would not affect repair frequency if the distribution of repairs remained relative (decreases in repairs of small gastropods were reciprocated by increases in repairs to larger gastropods) (Fig. 5.3B, C). Alternatively, repair frequency might be lower than expected if the loss of either small (more successful crabs) or large (less successful crabs) repairs was not proportional (e.g., small repairs are removed, but there are no comparatively large repairs gained) (Fig. 5.3H, I, K). Even if gastropods differ in size between sites, the observed number of repairs and comparison of repair frequencies will only be affected if the relative success of crabs (distribution of SAA) is different between the sites (Fig. 5.3D, E). In addition to our measures of crab strength (SAA), we therefore also assess relative crab success against the gastropods available to them by comparing the size distribution of repairs to the overall gastropod size distribution at each site.

To measure relative crab success between sites, we plotted histograms of both overall gastropod size (width) and size at attack (SAA), similar to methods used by Alexander and Dietl (2001), Mondal et al. (2014*b*), and Pruden et al. (2018). We then determined four values for each site: [1] the distance between the minimum repair size and minimum gastropod size (Fig. 5.3A), [2] the proportion of repairs that occurred below the minimum gastropod size (Fig. 5.3A), [3] of the repairs that overlapped with gastropod size at the site, the proportion of repairs that occurred between the minimum and median gastropod size at each site (Fig. 5.3A), and [4] the distance between the maximum repair size and maximum gastropod size at each site (Fig. 5.3A).

Both the distance between the minimum repair size and gastropod body size [1], as well as the maximum repair size and gastropod body size [4] represent the relationship between the range of repairs and the range of gastropods available to crabs at each site (Fig. 5.3A). Minimum repair size can be thought of as the minimum size at which crabs are likely to fail, resulting in a repair scar. Below that size range, we infer that crabs were 100% successful in crushing those small prey. At the other end of the distribution, maximum repair size indicates the maximum size of gastropod a crab might attack. Any gastropod body size above the maximum SAA likely indicates those gastropods are within a size refuge from crab predation (e.g., Alexander and Dietl 2001; Leighton 2002; Richards and Leighton 2012; Mondal et al. 2014*b*). If the distance between the minimum/maximum SAA and gastropod body size is different between samples, the observed repair frequency might not be comparable. For example, if the distance between the minimum SAA and gastropod body size was smaller in one sample, it would indicate that crabs were more successful against smaller crabs (the minimum SAA was relatively larger), and that there would be fewer repairs than expected compared to a site with a greater distance between the minimum SAA and gastropod body size (Fig. 5.3H). If the minimum SAA was found to shift relative to the minimum gastropod body size, the proportion of repairs below the minimum gastropod body size [2] would change (Fig. 5.3H), and could therefore be measured to get a rough estimate of how many repairs might be “missing” compared to other samples . Furthermore, examining where the majority of repairs occur relative to the mean gastropod size

[4] can also be used to see if success is shifted up or down when comparing sites (fewer attacks below the mean gastropod size might indicate stronger crabs that were less likely to fail on gastropods in that size range, or vice versa) (Fig. 5.3B, C). The proportion of repairs occurring above the median gastropod at each site was not calculated, as it would just be the inverse of the proportion of repairs occurring between the minimum and median gastropod size (Fig. 5.3A). Crab strength was estimated simply by the differences in the repair sizes (SAA) between sites, as determined above. We then ran K-W and Dunn tests on each of the four variables (referred to as measures of success) to test if success differed between any of the regions.

5.3 Results

5.3.1 Regional Effects

There were significant regional differences in repairs, gastropod size, and size at attack (SAA) (K-W test, $p < 0.01$) (Table 5.1). However, there were no obvious latitudinal patterns (Fig. 5.4). Sites within each region were most similar to one another. Repair frequency was highest in B.C. and lowest in southern California (Fig. 5.4A), with repair frequency significantly greater in B.C. compared to Oregon and southern California, as well as northern compared to southern California ($p < 0.05$) (Table 5.1). Snails in Oregon were significantly larger than snails from B.C. and southern California ($p < 0.05$) (Table 5.1), and nearly significantly larger than those from northern California ($p = 0.055$) (Table 5.1, Fig. 5.4B). Snails were also repaired at larger sizes in Oregon ($p < 0.05$) (Table 5.1, Fig. 5.4C).

5.3.2 Influences on Repairs and Size at aAtack

For models of RF at the site level, region was the only factor to predict RF significantly, and not size or the size of attacks (Table 5.2, Fig. 5.5A, B). However, at the individual level, size did significantly predict whether a gastropod had at least one scar. Scarred gastropods were significantly larger than unscarred gastropods (Table 5.2, Fig. 5.4D), and gastropod size was also significantly larger as the number of scars increased (Table 5.2). But, this relationship between scars and size was constant between sites (Fig. 5.4D), as RF was not influenced by size (Fig. 5.5A), suggesting that at each site, failure/scars were more likely to occur as size increased. Partial correlations controlling for regional differences indicated the same results, with no significant correlations between RF and size, but a small, significant effect of size on the presence and number of scars (partial R = 0.0635, 0.0585, respectively $p < 0.0001$) (Fig. 5.4D).

Size of attacks (SAA) were also significantly explained by the size of gastropods at each site (Table 5.2, Fig. 5.5C). When controlling for regional differences in SAA and size, we found that there was a strong partial correlation between SAA and size (width) (partial R = 0.8806, $p < 0.0001$) (Fig. 5.5C).

5.3.3 Patterns of Crab Strength/Relative Success

Not only did repairs in Oregon occur at larger sizes (SAA was significantly larger), but there were also fewer repairs at relatively small sizes when compared to the overall distribution of gastropod sizes (Tables 5.1, 5.3, Fig. 5.6B). The distance between the minimum repair size and minimum gastropod size [1] was significantly smaller in Oregon compared to B.C. and northern California (Table 5.1, Fig. 5.6). Oregon also had significantly fewer repairs in this size range [2] (below the minimum gastropod size at each site), with an average of 4% of the repairs, compared to 30% in B.C. and northern California (Tables 5.1, 5.3, Fig. 5.6). Furthermore, of the repairs that overlapped with gastropod size at each site, there were more repairs in the larger size range [3] in Oregon compared to B.C., although the K-W test for all regions was not significant (Table 5.1, Fig. 5.6). Southern California was an intermediate, with 20% of the repairs occurring below the minimum gastropod size [2], but showing no statistically significant differences any of the other regions for any of the measures of success (Table 5.1, Fig. 5.6D). The maximum size of repairs was not statistically distinguishable between any of the regions (Table 5.1).

5.4 Discussion

By examining only one wide-ranging prey species (and therefore ensuring defense capabilities of prey are comparable), we were able to establish a baseline of how repair scars systems can be assessed across a broad geographic coastline. Along the west coast of Canada and the U.S., we found that for *T. funebralis,* repair frequency, gastropod size, and size of attacks all showed regional, rather than latitudinal patterns, with Oregon showing the greatest differences among regions. Between sites, repair frequency was also unaffected by differences in size or the size of attacks, but within each site, larger gastropods were more likely to have at least one repair scar. We also found a strong correlation between size of attacks and overall prey size at each site, suggesting that crab failure is more likely as gastropod size increases at each site. Crabs in Oregon are also relatively more successful, with fewer failures (repairs) on the smaller gastropods available to them compared to the other regions. Repair frequency might therefore be lower than expected in Oregon compared to the other regions. However, as there are more large gastropods in Oregon, repair frequency may not be affected as much as expected by the loss of small repairs because the relative proportions and distribution of repairs are similar between regions, with only the loss of smaller repairs showing disproportionate reductions in Oregon compared to the other regions. Repair scars on crab prey are therefore a useful dataset for understanding patterns of crab predation across multiple spatial and temporal scales.

5.4.1 Regional Patterns

Our results indicate that there are strong regional patterns in both *T. funebralis* and crabs along the west coast of Canada and the U.S. Despite the range of habitats and conditions captured at localities in each region, sites from the same region tended to plot more closely to one another than to sites in other regions for all of our dependent variables (Figs. 5.4, 5.5). However, the observed regional patterns did not correspond to broad latitudinal gradients in either crab predation or prey body size. Oregon in particular disrupted any potential latitudinal patterns, as repair frequency there was lower than might have been expected for a latitudinal predation gradient, and gastropods were larger compared to the other three regions. Even when evaluating relative success and crab strength, Oregon was different from the other regions, with gastropods not only being repaired at larger sizes (SAA), but crabs also being relatively more successful, at least against the smaller gastropods available to them. Variation in regional conditions along the west coast of Canada and the U.S. is therefore more influential over crab populations and patterns of repair scars and body size in *T. funebralis* than any potential latitude gradients. Other studies have also found regional patterns along the west coast of North America due to upwelling and coastline shape (Menge et al. 2004; Cooper and Shanks 2011), interacting environmental conditions (Kroeker et al. 2016), and the presence of habitat forming species (Jurgens and Gaylord 2018).

Whether or not a change in the number of repair scars is influenced by success, if one expected a latitudinal gradient of increasing predation from north to south, the change in repairs should be consistent with latitude. Instead, predation varied more by region. Similar to RF, there were also no latitudinal trends in the size of snails that were repaired. If one expected there to be a latitudinal trend towards more powerful predators at lower latitudes, regardless of body size, an increase in the size of attacks should have been observed with decreasing latitude. Instead, size at attack tracked overall gastropod size in each region, with SAA being significantly larger in Oregon compared to both B.C. and northern California, but not significantly different between B.C., northern, or southern California. Predation is therefore influenced by regional conditions, and there is no evidence of latitudinal predation gradients in either repair frequency or size of attacks.

Furthermore, there were no latitudinal trends in gastropod body size, nor was body size related to repair frequency. For example, sites in B.C. had an average repair frequency of 64%, while sites in southern California averaged 20%, yet *T. funebralis* from both regions were similar in size. Only Oregon *T. funebralis* were different, with significantly larger individuals than any other region, regardless of repair frequency. Other studies of *T. funebralis* have found that populations in the same area of Oregon tend towards more and larger adults (>9 g) than do sites to the south, which contain more smaller individuals (Cooper and Shanks 2011). Another study of *T. funebralis* also found that snails in Oregon were larger than snails in California (Frank 1975). Frank (1975) also concluded that snails from B.C. were larger than those from California, although this was based on a single site from Bamfield, which was in a size range comparable to those sites near Bamfield from the present study, so it is plausible that *T. funebralis* found near

Bamfield are actually more comparable to individuals from California than Frank initially surmised. We therefore caution that latitudinal trends between “north” and “south” *T. funebralis* are more a function of studies taking places within mainland U.S. rather than a real latitudinal gradient. The similarity in body size between snails in B.C. and California suggests that body size is not related to latitude (although we recognize that our sites from B.C. were all in a small geographic area near Bamfield in Barkley Sound, and might not be reflective of other northern areas). More study of *T. funebralis* body size along the coast of B.C. and Alaska is needed to elucidate any potential relationship between body size and latitude in *T. funebralis*.

Regardless of the reason behind the observed patterns of repairs and size in *T. funebralis*, our results also suggest that region is an important factor to include when examining broad-scale patterns in predation. In particular, when trying to observe how repair frequency and the size of attacks might be influenced by other factors, such as size, regional variation obscured the underlying relationships between variables. For example, without including region in our models, RF showed a nearly significant negative correlation with both height and SAA ($R = -0.35$, $p = 0.06$) across the entire study area, but this pattern was not true or recognizable once region was included (Table 5.2, Fig. 5.5A, B). By controlling for regional variation, we were able to determine underlying relationships between repairs, body size, and size at attack that are critical to determining what might influence crab success and the formation of repair scars across a broad geographic range.

5.4.2 Overall Patterns in Predation

Despite regional differences, repair frequency was not influenced by either size or size of attack, suggesting that RF likely represents the number of attacks at each site, at least for B.C., northern, and southern California, where there are no significant differences in the relative distributions of repairs. In contrast, at the level of the individual, crab failure (and therefore the occurrence of a repair scar) was driven by size, with larger gastropods within each site more likely to have at least one scar. This suggests that, regardless of differences in sizes of gastropods between sites, crabs were simply more likely to fail on larger specimens at each site, and/or that larger gastropods at each site have had more time to accumulate scars (Vermeij 1987; Dietl and Kosloski 2013; Stafford et al. 2015*a*). Even if repair frequency and gastropod body size differs between sites, crabs were still more likely to fail on the larger gastropods at each site, therefore the probability of failure remained relative, which might explain why repair frequency was not necessarily related to size. Furthermore, SAA was strongly related to size, also suggesting that crab failure was proportional to the size of the gastropods available to them at each site. Given that observed failures seem to be proportional across all sites, and that RF was not influenced by size or size at attack, this suggests that any observed differences in repair frequency should therefore be attributed to differences in the amount of crab predation at each site. Sites in Oregon still followed the same trend, but as a region, may have had lower repair frequencies than expected given that we did see increases in the relative strength of crabs in Oregon.

5.4.3 Patterns of Success

Even though the size of attacks were strongly tied to the size of the gastropods at each site, measuring the differences in relative success between regions provided more detailed estimates of how repair frequency might be affected by a change in success. For example, if there were two regions with differently sized gastropods, but the size and distribution of repairs remained relative to the gastropods in each region, repair frequencies would be reflective of attack rates, as there were no differences in the relative success of the crabs compared to the gastropods available to them (Fig. 5.3B vs D, C vs. E). Crabs in Oregon were more successful than in other regions, both in terms of their strength (larger SAA), as well as their relative success compared to the gastropods in their region (proportionately fewer repairs on small gastropods) (Fig. 5.6). Neither crab strength (SAA) nor relative crab success showed significant differences between B.C., northern, and southern California, although southern California crab success might have been slightly greater, given that there were 10% less repairs at smaller sizes than B.C. or northern California (20% vs. 30%), although this was not statistically significant (Fig. 5.6). However, even though gastropods in Oregon were attacked at larger sizes (Fig. 5.6B), because the gastropods themselves were also larger, the distribution of repairs in Oregon remained somewhat relative, with only the loss of repairs below the minimum gastropod size (e.g., Fig. 5.3H). Therefore, RF in Oregon might not have changed as much as one might have expected because there are still the same proportion of repairs observed at larger sizes (Fig. 5.6). The same was true for southern California, where the distribution of repairs was the same as B.C. and northern California, with a possible loss of repairs only occurring in that same smallest repair size range (Fig. 5.6). Our results indicate that repair frequency and success can potentially be evaluated independently, so long as the size and relative distribution of repairs compared to prey size is known.

As crabs appeared more successful in killing smaller gastropods in Oregon, with fewer observed small repairs and a shift towards repairs at relatively larger sizes compared to other regions, repair frequency in Oregon and southern California may be lower than expected compared to B.C. and northern California. If we wanted to compare attack frequency more accurately between the regions, we could potentially correct for the “missing” repairs in the small size range (small gastropods that were killed and removed) by adding the “missing” repairs back into Oregon and southern California so they were more comparable to B.C. and northern California. We propose a relative correction for our dataset that would determine the number of “missing” repairs in Oregon and southern California compared to the other two regions by first determining the differences in the proportion of small repairs between the regions [2], and using that value to determine the number of “missing” repairs (observed repairs * proportion of repairs missing in Oregon or southern California compared to B.C. and northern California). Once we had determined this “missing” number of repairs, we could recalculate repair frequency by adding the “missing” repairs back into both the numerator (number of observed repairs + “missing” repairs) and denominator (number of observed gastropods + “missing” repairs (or gastropods)). For example, there were 26% less repairs below the minimum gastropod size [2] in Oregon compared to B.C. and northern California (4% compared to 30%), so we would multiply the observed repairs by 0.26 to determine the number of “missing” repairs at each site in Oregon, and then add those repairs into the numerator and denominator when calculating the “corrected” repair frequency. Note that this method is not an attempt to determine the actual number of attacks experienced in any region, but simply tries to back out the differences in relative success to make repair frequencies more comparable between the regions. When adding the correction for RF, we find that the results of our original K-W tests of RF and region do not change, and Oregon and southern California increase their RF only slightly (Table 5.1). This supports our hypothesis that success may not affect observed repair frequencies as much as has been suggested in the past (Leighton 2002; Alexander and Dietl 2003). Furthermore, this may explain why some studies have found repair frequency to indicate the number of attacks, rather than success (Schindler et al. 1994; Molinaro et al. 2014; Stafford et al. 2015*a*).

5.4.4 Potential Drivers of Observed Patterns

As in the fossil record where access to information on predators is limited and therefore must be inferred from proxies, such as repair scars, we can use similar proxies to identify patterns in predators today, regardless of the cause. While there are many possible explanations for the strong regional patterns observed in crab repairs and success, at least some of our patterns follow previous patterns attributed to oceanographic conditions influencing predation along the California Current system. For example, areas with strong upwelling in northern California are known to have greater rates of predation than areas with weak upwelling (e.g., Southern California) (Menge et al. 2004), which matches the patterns we observed. Furthermore, the intermittent upwelling and proximity of the California Current to shore in Oregon are thought to retain more larvae than areas like northern California where upwelling is strong and the California Current is further offshore (Menge et al. 2004), potentially leading to different patterns of recruitment that might affect population structure of crabs in Oregon compared to other regions. However, it is important to note that *T. funebralis* are not be affected in the same way, as recruitment in *T. funebralis* appears greater in California than Oregon, possibly due to their shorter larval duration compared to crabs and sea stars (Cooper and Shanks 2011).

Crab repair frequency (RF) may not only follow general patterns of oceanographic currents, but RF is also known to be associated with wave energy, with quieter water sites having greater repair frequencies and more crabs/crab attacks than more wave-exposed sites due to longer foraging times in the former setting (Molinaro et al. 2014; Stafford et al. 2015*a*). As sites from B.C. were from within a sound (Barkley Sound) rather than along the open coast, reduced wave energy could explain the greater repair frequencies observed in B.C. compared to Oregon and southern California, but not necessarily northern California. Another possibility is that age in *T. funebralis* is thought to follow latitude, with individuals in the southern part of their range (e.g., southern California) living an average of 7 years, compared to individuals in Washington/Oregon that are thought to live 30 or more years (Paine 1969*b*; Frank 1975; Cooper and Shanks 2011). Age may minimally explain the reduced repair frequencies in southern California, but as northern California and Oregon do not fit this trend, age alone is not a sufficient explanation for the reduced repair frequencies observed in both Oregon and southern California.

Human activity may be another possible explanation for the patterns of RF observed, at least for the reduced repair frequencies in southern California. A recent study has suggested rock crabs may be becoming overfished in southern California (Fitzgerald et al. 2018). At each of our seven sites in southern California, there was a noticeable absence of rockweed and macroalgal cover compared to all other sites included in the study. Most of the *T. funebralis* were found on bare rock, presumably feeding on the relatively thick biofilm and any kelp that washed into the sites. Rockweed populations have begun to decline in southern California in recent years (Whitaker et al. 2010). Rock crabs, particularly juveniles and females, tend to live and hunt in areas that have sufficient cover, such as cobbles or macroalgae, to protect them from their own predators, with only the largest males observed hunting in more exposed settings (Robles et al. 1989; Behrens Yamada and Boulding 1996; Behrens Yamada and Groth 2016). A lack of macroalgae could therefore explain the low predation frequency observed in southern California sites.

In terms of success, our results suggest that crabs in Oregon (and possibly Washington) may be larger and stronger than other regions. While there are currently no catch size limits for rock crabs in Oregon, catch size limits of red rock crabs (*Cancer productus*) in Washington are larger than those in B.C., and California (Behrens Yamada and Groth 2016). Furthermore, anecdotal observations in both Washington and Oregon indicate that most crabs exceeded 120 mm (Behrens Yamada and Groth 2016), which is potentially larger than other areas. Furthermore, crab size, and by extension, strength, might be a more important selective pressure on prey than predation frequency, leading to larger *T. funebralis* in Oregon. Predation has a binary outcome – either the attack is successful and the prey is consumed, or it is not and the prey survives. In the case of gastropods, a failed attack does not dictate subsequent growth or growth rates (unless the mantle tissue was irreversibly damaged). Therefore, if repair frequency is simply a reflection of predator abundance, regardless of success, any individual which survives an attack can still grow and reproduce. However, if the crabs are comparatively larger, as in Oregon, regardless of predation frequency, only those larger snails will survive attacks, as more smaller individuals will be successfully crushed, meaning that snails which grow larger could have more chances to reproduce. Larger crabs in Oregon could also explain the larger *T. funebralis* observed in that region; bigger, stronger predators would select for bigger prey (Vermeij 1982*a*). These results provide a framework for investigating such potential patterns of selection across broader temporal scales in the fossil record.

There are many further questions that could be tested to explain the observed patterns in *T. funebralis* and their repair scars along the west coast of Canada and the U.S., but what remains clear is that by controlling for prey species/defense capabilities, we are able to use repair scars as a means of determining patterns of crab predation along a latitudinally extensive coastline. Our results indicate that there are strong regional, rather than latitudinal patterns of crab predation, and that by measuring the size of attacks, we can measure differences in both the strength and relative success of the predators, as well as how relative success may/may not affect repair frequency. Without detailed information on predators themselves, such as crabs, studies of predation traces left on prey therefore provide useful information on predators when information on predators is limited or lacking, both in modern ecological and palaeontological studies.

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Table 5.1

Kruskal – Wallis test results including pairwise Dunn tests with Bonferroni correction of the four regions. Significant p-values are in bold. K-W and Dunn test results for success measures (1 – 4, as specified in Fig. 5.3) and “corrected RF_1” are also included.

				B.C. - Oregon		**B.C. - Nor. Cal**		**B.C. - So. Cal**		**Oregon - Nor. Cal**		**Oregon - So. Cal**		**Nor. Cal - So. Cal**	
	K-W X^2	**DF**	**p-value**	**z stat.**	**p**	**z stat.**	**p**	**z stat.**	**p**	**z stat.**	**p**	**z stat.**	**p**	**z stat.**	**p**
RF_1	18.8650	3	**0.0003**	2.8568	**0.0128**	0.5064	1.0000	3.8463	**0.0004**	-1.9991	0.1368	1.0864	0.8320	2.9066	**0.0110**
Width	16.6624	3	**0.0008**	-3.2823	**0.0031**	-0.5224	1.0000	0.5117	1.0000	2.3563	0.0554	3.6827	**0.0007**	0.9610	1.0000
SAA	17.2233	3	**0.0006**	-3.8293	**0.0004**	-0.7783	1.0000	-0.5621	1.0000	2.5802	**0.0296**	3.1374	**0.0051**	0.2610	1.0000
Success measures															
[1] Dist. min SAA - Width	18.8904	3	**0.0003**	3.9058	**0.0003**	0.2586	1.0000	2.3555	0.0555	-3.1671	**0.0046**	-1.4179	0.4686	1.8302	0.2017
[2] % SAA < min Width	14.6310	3	**0.0005**	3.7083	**0.0006**	-0.1440	1.0000	1.3046	0.5760	-3.3963	**0.0020**	-2.2779	0.0682	1.2933	0.5877
[3] % SAA min - mean Width	6.9901	3	0.0722												
[4] Dist. max SAA - Width	2.1812	3	0.5357												
"Corrected" RF_1	16.0490	3	0.0011	2.4617	**0.0415**	0.5438	1.0000	3.6659	**0.0007**	-1.6153	0.3187	1.2877	0.5936	2.7108	**0.0201**

Table 5.2

Generalized linear models of RF and SAA for locality data, and mixed models of the presence/absence of a scar and number of scars for individual data. Model performance was compared by log-likelihood ratio tests ("vs." indicates which models were compared), with the best models indicated by lower AIC scores. For mixed models, locality was added as a random effect. Significance of the independent variables (coefficients) from the full models was assessed using t values (generalized linear models) and Wald Z-test scores (mixed models), with significant values for region indicating significant differences between those regions.

Generalized linear models of site averages

RF_1 models (family = gaussian)

Model	**AIC**	**Resid. Df**	**Resid. Dev**	**Df**	**Deviance**	**Pr(>Chi)**	**vs.**
Null	-2.372	27	1.3057				
Region only	**-26.284**	24	0.4487	3	0.8571	**<0.0001**	Null
Full (Region + Width + SAA)	-25.150	22	0.4050	5	0.9008	**<0.0001**	Null
				2	0.0437	0.3055	Region

Coefficients from full model	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Width	-0.0537	0.0364	-1.477	0.1540
SAA	0.0374	0.0342	1.093	0.2863
B.C. vs. Oregon	-0.3451	0.1328	-2.598	**0.0164**
B.C. vs. Nor. Cal	-0.1458	0.0808	-1.803	0.0851
B.C. vs. So. Cal	-0.5024	0.0861	-5.832	**<0.0001**
Oregon vs. Nor. Cal	0.1993	0.1199	1.663	0.1105
Oregon vs. So. Cal	-0.1574	0.1152	-1.366	0.1859
Nor. Cal vs. So. Cal	-0.3567	0.0865	-4.123	**0.0004**

SAA models (family = gaussian)

Model	**AIC**	**Resid. Df**	**Resid. Dev**	**Df**	**Deviance**	**Pr(>Chi)**	**vs.**
Null	147.680	27	277.4900				
Region only	115.140	24	70.0610	3	207.4300	**<0.0001**	Null
Full (Region + Width)	**75.311**	23	15.7280	4	261.7700	**<0.0001**	Null
				1	54.3340	**<0.0001**	Region

Coefficients from full model	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Width	0.9356	0.1050	8.914	**<0.0001**
B.C. vs. Oregon	2.5300	0.6140	4.120	**0.0004**
B.C. vs. Nor. Cal	0.6117	0.4758	1.286	0.2114
B.C. vs. So. Cal	1.4354	0.4314	3.328	**0.0029**
Oregon vs. Nor. Cal	-1.9182	0.6113	-3.138	**0.0046**
Oregon vs. So. Cal	-1.0945	0.6642	-1.648	0.1129
Nor. Cal vs. So. Cal	0.8237	0.4985	1.652	0.1121

Mixed models of individuals

Presence/absence of a scar (family = binomial)

Model	**AIC**	**BIC**	**logLik**	**Resid. Df**	**Resid. Dev**	**Chisq**	**Chi DF**	**Pr(>Chi)**	**vs.**
Null	5702.4	5715.3	-2849.2	4792	5698.4				
Region only	5680.1	5712.5	-2835.1	4789	5670.1	28.253	3	**<0.0001**	null
Full (Region + Width)	**5639.3**	5678.1	-2813.6	4788	5627.3	71.116	4	**<0.0001**	null
						42.863	1	**<0.0001**	Region

Random effects	**Name**	**Variance**	**Std. Dev**
Locality	(Intercept)	0.4309	0.6564

Coefficients from full model	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Width	0.0867	0.0134	6.478	**<0.0001**
B.C. vs. Oregon	-1.9160	0.3474	-5.515	**<0.0001**
B.C. vs. Nor. Cal	-0.7297	0.3875	-1.883	0.0597
B.C. vs. So. Cal	-2.1403	0.3575	-5.987	**<0.0001**
Oregon vs. Nor. Cal	1.1863	0.3872	3.064	**0.0022**
Oregon vs. So. Cal	-0.2243	0.3588	-0.625	0.5319
Nor. Cal vs. So. Cal	-1.4106	0.3977	-3.546	**0.0004**

Number of scars (family = Poisson)

Model	**AIC**	**BIC**	**logLik**	**Resid. Df**	**Resid. Dev**	**Chisq**	**Chi DF**	**Pr(>Chi)**	**vs.**
Null	8655.9	8668.9	-4326	4792	8651.9				
Region only	8630.4	8662.7	-4310.2	4789	8620.4	31.555	3	**<0.0001**	Null
Full (Region + Width)	**8561.8**	8600.6	-4274.9	4788	8549.8	102.150	4	**<0.0001**	Null
						70.600	1	**<0.0001**	Region
					Random effects		**Name**	**Variance**	**Std. Dev**
					Locality		(Intercept)	0.1817	0.4263
			Coefficients from full model			**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
			Width			0.0667	0.0079	8.447	**<0.0001**
			B.C. vs. Oregon			-1.3383	0.2228	-6.007	**<0.0001**
			B.C. vs. Nor. Cal			-0.4178	0.2485	-1.681	0.0927
			B.C. vs. So. Cal			-1.4911	0.2326	-6.409	**<0.0001**
			Oregon vs. Nor. Cal			0.9205	0.2514	3.661	**0.0003**
			Oregon vs. So. Cal			-0.1528	0.2371	-0.644	0.5193
			Nor. Cal vs. So. Cal			-1.0733	0.2610	-4.113	**<0.0001**

Table 5.3

Summary data for each locality. “# Attacked” = snails with at least one scar, “# Attacks” = total number of scars. Success measures (1 – 4, as specified in Fig. 5.3) and “corrected” RF_1 are also included. Map of the localities listed is shown in Fig. 5.2.

Region	Locality	Height	Width	SAA	RF_1	RF_2	Sample Size	# Attacked	# Attacks	[1] Min SAA - w	[2] % SAA < min w	[3] % SAA min - mean w	[4] Max SAA - w	"Corr." RF_1
B.C.	Dixon Island Exposed	17.28	20.40	16.05	0.78	1.28	120	93	154	7.57	0.4481	0.7059	1.78	0.7750
	Dixon Island Sheltered	19.50	21.96	19.05	0.86	1.55	120	103	186	7.92	0.2473	0.6738	0.46	0.8583
	Scott's Bay	17.33	20.95	17.50	0.67	1.03	120	80	123	7.20	0.1870	0.8200	3.36	0.6667
	Strawberry Point	18.28	19.98	16.94	0.93	2.63	120	112	315	10.09	0.1238	0.6731	0.61	0.9333
	Mather's Bay	15.63	20.28	15.20	0.59	0.88	120	71	105	6.91	0.5000	0.7297	2.46	0.5966
	Brady's Beach South	20.19	24.82	21.09	0.55	0.76	120	66	91	8.78	0.3889	0.7609	5.44	0.5500
	Prasiola Point	16.18	20.64	16.38	0.42	0.59	120	50	71	7.35	0.3521	0.7091	1.26	0.4167
	Nudibranch Point	18.79	24.02	20.84	0.32	0.40	119	38	48	5.90	0.2292	0.7645	0.68	0.3167
Oregon	Boiler Bay	22.92	24.36	22.92	0.20	0.24	221	45	53	1.79	0.0566	0.6600	1.16	0.2444
	Yaquina Head	23.62	24.96	23.96	0.33	0.36	217	72	79	2.17	0.0253	0.5888	0.08	0.4234
	Quarry Cove	27.86	27.63	25.05	0.29	0.34	210	61	71	4.79	0.1408	0.6863	0.90	0.3569
	Strawberry Hill	23.93	25.83	24.46	0.44	0.55	196	87	108	0.00	0.0092	0.6667	1.40	0.4911
	Bob's Creek	22.04	24.21	23.77	0.31	0.34	201	62	69	0.92	0.0000	0.5692	3.98	0.3558
	Sunset Bay	26.37	25.48	23.64	0.36	0.44	201	72	89	-0.09	0.0000	0.5217	1.04	0.4138
	Cape Arago South Bay	26.64	26.76	24.36	0.24	0.28	200	47	56	0.99	0.0893	0.6282	1.27	0.2591
	Cape Blanco	27.14	28.42	27.50	0.29	0.32	204	59	66	4.78	0.0152	0.7377	1.41	0.3307
Nor. Cal	Duncan's Cove	19.53	22.93	20.31	0.51	0.72	201	102	145	9.50	0.3241	0.6667	3.52	0.5050
	Carmet Beach	20.34	23.07	19.91	0.39	0.50	202	79	100	7.02	0.3700	0.6566	1.83	0.3930
	Mussel Point	17.46	20.16	16.57	0.43	0.54	209	89	113	5.19	0.2301	0.8966	0.57	0.4258
	Horseshoe Cove	19.72	22.17	19.60	0.56	0.77	213	120	164	8.43	0.2561	0.6940	3.84	0.5769
	Campell Cove	20.53	22.91	18.96	0.63	0.98	208	132	204	6.61	0.3399	0.7705	1.99	0.6197
So. Cal	Abalone Cove NW	20.41	21.42	19.98	0.33	0.37	183	61	67	4.03	0.1045	0.6275	3.42	0.4401
	Pelican Cove	16.49	18.90	16.12	0.14	0.17	149	21	26	7.92	0.3077	0.7000	4.27	0.1408
	Abalone Cove Centre	20.43	22.28	19.08	0.11	0.12	159	18	19	4.00	0.3158	0.7347	2.63	0.1153
	White Point Park	18.89	19.92	18.89	0.11	0.12	180	20	21	5.08	0.1429	0.7778	2.87	0.1466
	Sun Gold Point	23.59	23.54	20.96	0.25	0.32	171	42	54	2.30	0.0926	0.7143	3.32	0.2846
	Bird Rock Point	20.13	22.00	18.27	0.14	0.17	163	23	27	3.88	0.2593	0.6833	0.34	0.1374
	False Point	17.98	19.76	18.55	0.31	0.42	147	46	61	2.42	0.1667	0.5000	0.67	0.2756

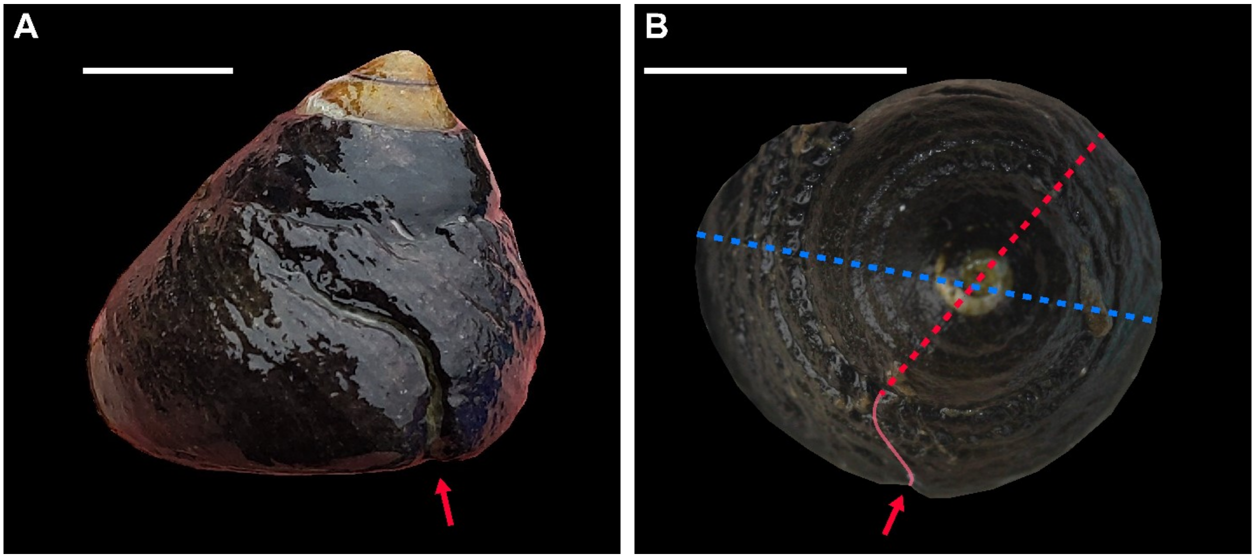

Figure 5.1

Examples of repair scars on *T. funebralis* and their measurement. A. A typical repair scar generated by a failed apertural peel by a crab (red arrow), attributed to the ichnogenus *Caedichnus* (Stafford et al. 2015*b*). **B.** Size of the gastropod at the time of attack (SAA), measured from where the scar (red arrow, traced by red line) met the top of the whorl where it occurred along a line segment through the centre of the gastropod to the opposite edge of the shell (red dotted line). Overall body width measurements were taken as the maximum width (diametre) of the gastropod shell (blue dotted line).

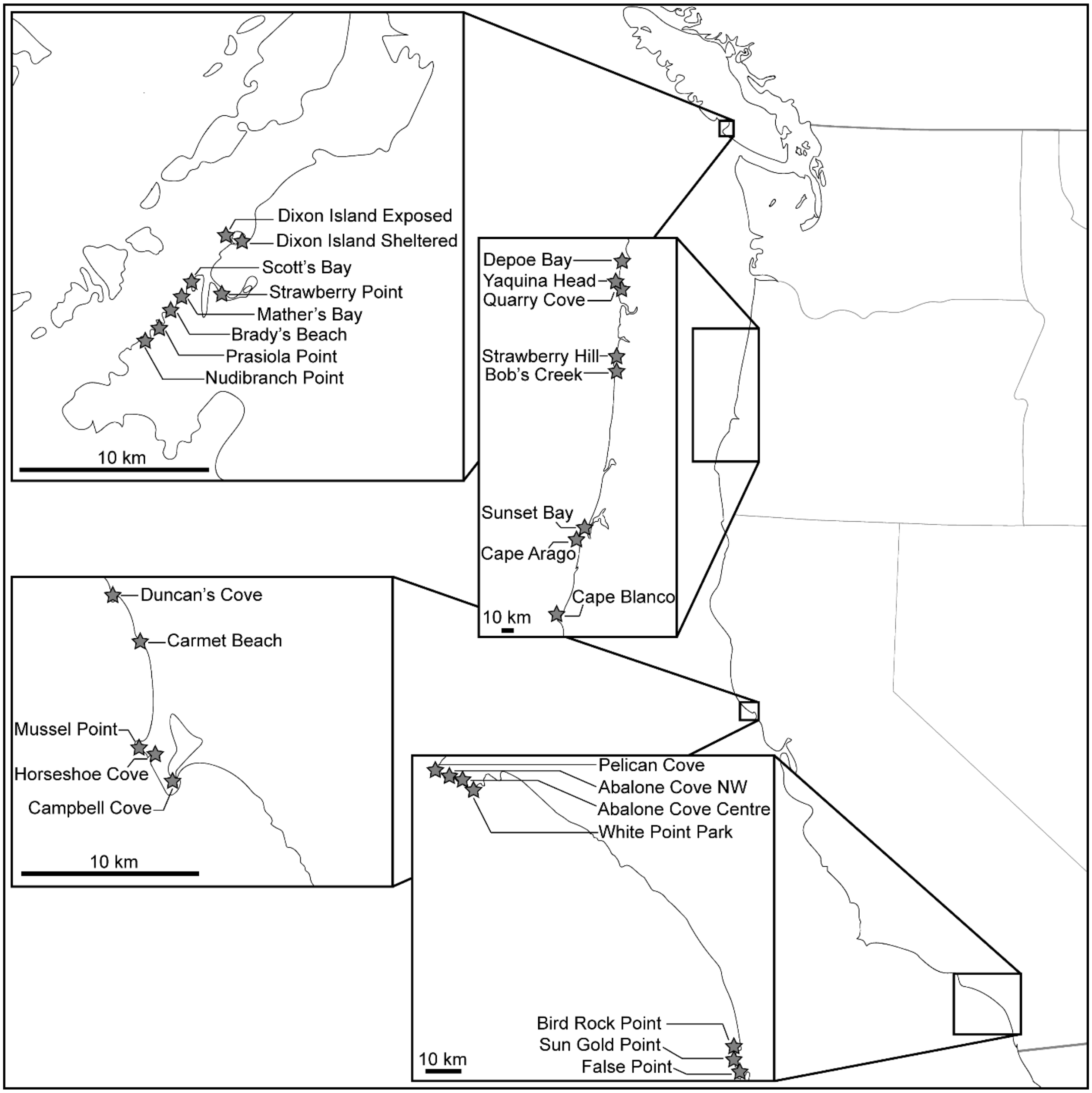

Figure 5.2

Map of the west coast of Canada and the U.S. showing the four regions sampled, with inset maps of each region showing the location of the 28 sampled sites in more detail. Regional inset maps are arranged from the top to bottom of the figure based on latitude (B.C., Oregon, northern California, southern California). Localities are indicated by grey stars with the name of the locality included. Scale bar in each inset is 10 kms. Details of data collected from each site can be found in Table 5.3.

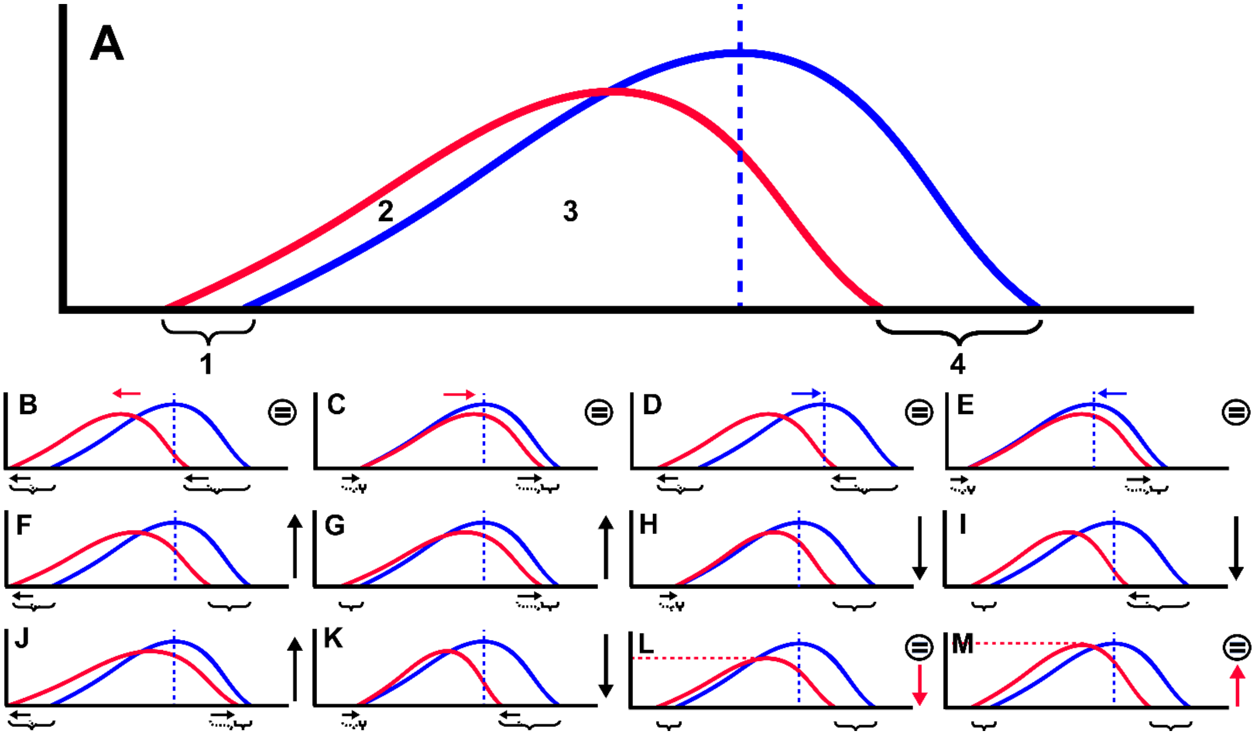

Figure 5.3

Hypothetical distributions of repair scar sizes (SAA) (red line) and overall prey body size (blue line) as they relate to predator success and comparability of repair frequency (RF) between samples. A. Null distributions of SAA vs. body size used to compare with other scenarios (fig. panels). Potential measures of success for comparison: [1] distance between minimum SAA and body size (minimum size at which predators are likely to fail, resulting in a repair), [2] proportion of repairs below the minimum prey size, [3] proportion of repairs between the minimum and mean (blue dotted line) prey size, and [4] distance between the maximum SAA and prey size (indicating the largest prey the predator is able to attack). **B. – E.** Red arrow = changes in predator strength, blue arrow = changes to prey size. Because the shift in the distribution of SAA or prey size is proportional ([1] and [3] remain relative), RF is not affected (equal symbol to right of graph). **F. – K.** Scenarios where the shift in the distribution of repairs is not proportional, indicating that RF might be affected (black arrows to right of panel indicate whether RF is greater or less than expected). **L and M.** If distributions of SAA and prey size are relative between samples, changes to RF = differences in the number of attacks (red dotted line).

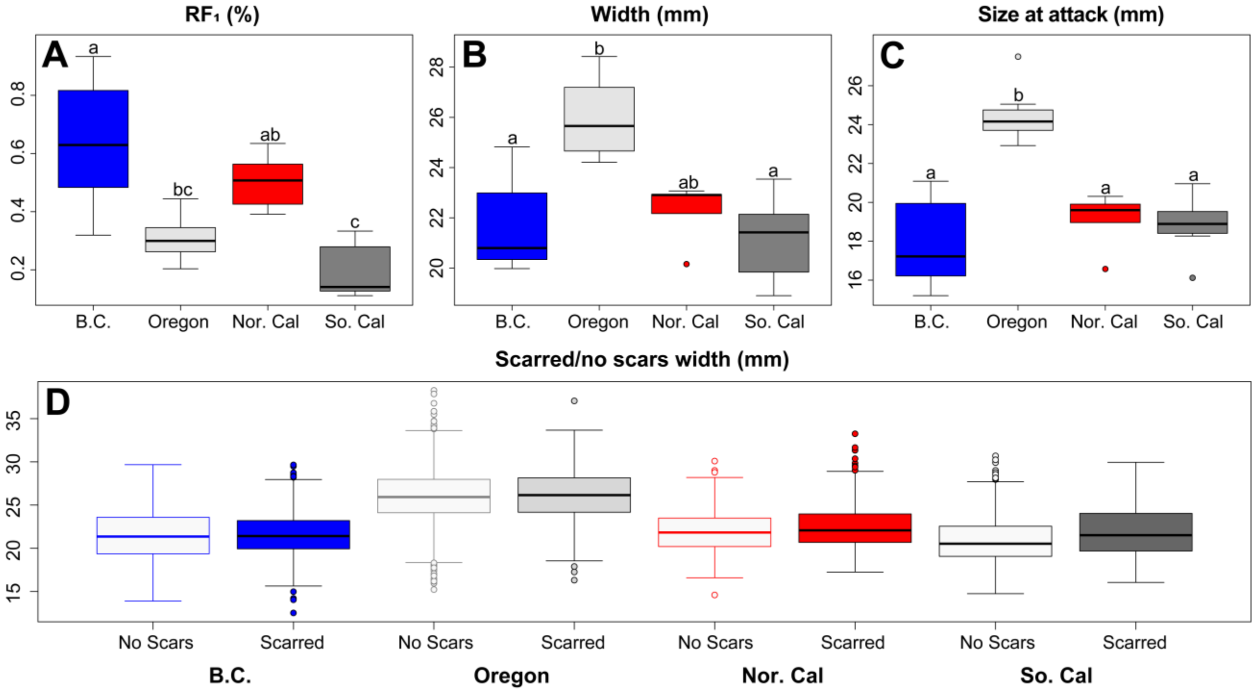

Figure 5.4

Boxplots showing regional differences in the number of repairs, gastropod size, and size at attack (SAA). A. Repair frequency (RF_1). **B.** Gastropod body size (maximum width). **C.** SAA. **D.** Size differences between unscarred and scarred gastropods for each region. Significantly different groups are distinguished by lowercase letters above the whiskers (panels A – C). Boxes = upper and lower quartiles, central lines = medians, whiskers = min/max data, circles = outliers.

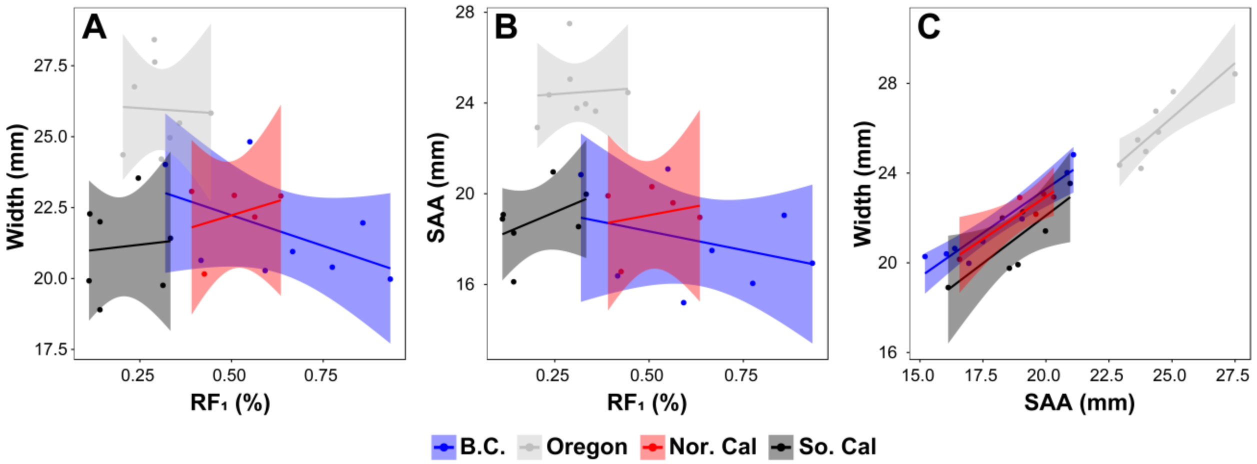

Figure 5.5

Scatterplots showing relationships between variables (Repair frequency, gastropod size, and SAA) with regional confidence intervals (95%) represented. A. Repair frequency (RF_1) vs. gastropod size (width), and **B.** RF_1 vs. SAA. RF is not affected by either gastropod size or SAA (Table 5.2). **C.** SAA vs. gastropod size (width) shows a strong positive correlation (partial R = 0.881, $p < 0.001$), despite regional differences in either variable.

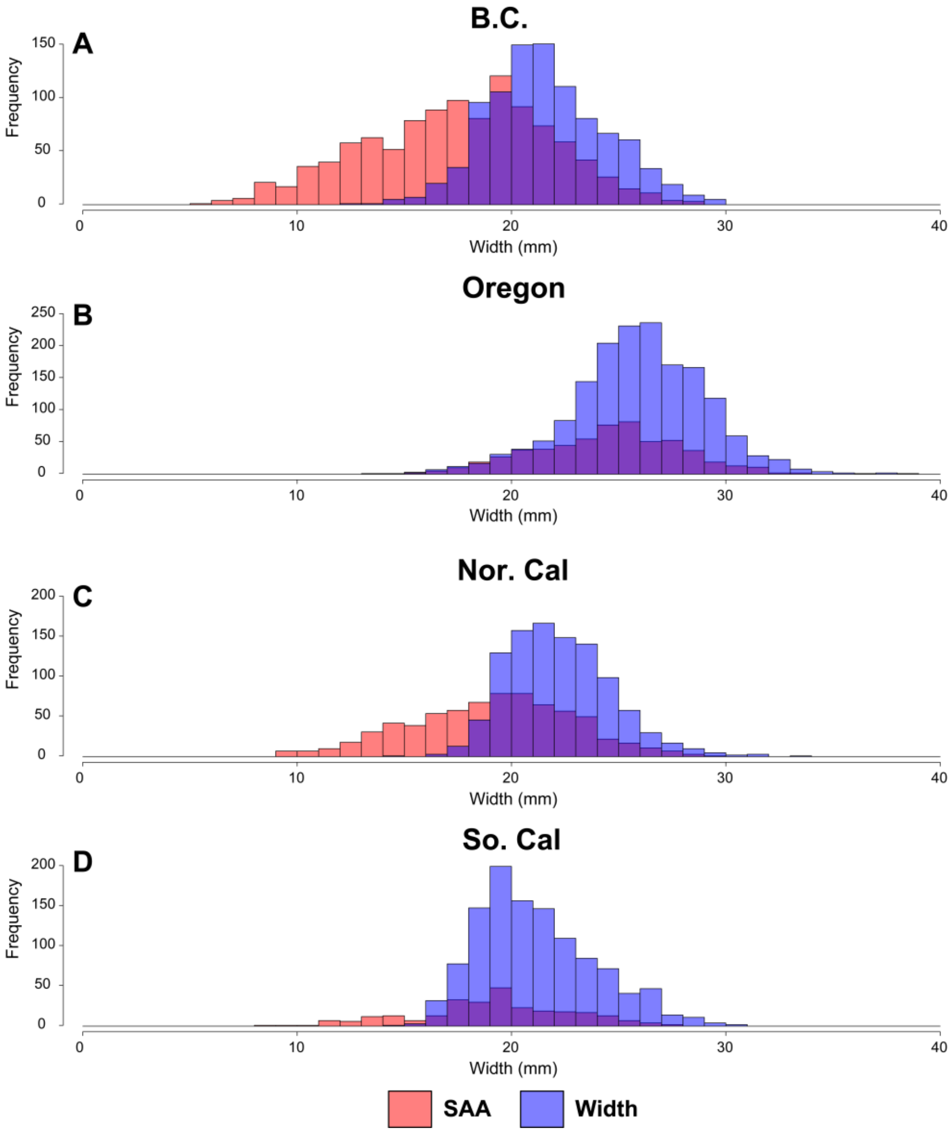

Figure 5.6

Regional histograms of SAA (red) and gastropod body size (blue) measurements. A. B.C. **B.** Oregon. **C.** Northern California. **D.** Southern California. Relative distributions of SAA and body size between regions can be compared based on Fig. 5.3 to determine crab strength, relative success, and how repair frequency might be affected. Gastropods in Oregon are larger, but crab strength (SAA) is also greater. The only significant differences in the distributions of SAA vs. size between regions is a loss of repairs at smaller sizes in Oregon (distance between min. SAA and size [1] and the proportion of repairs less than min. body size [2]). Repair frequency is likely slightly lower than expected in Oregon compared to the other regions (~26% fewer repairs on small gastropods).

Chapter 6

Crab predation scars as an indicator of changes to crab populations and gastropod prey since the Pleistocene

6.1 Introduction

Predation is an important component of selection and regulation in most ecosystems (Paine 1966, 1969*a*; Pianka 1966; Vermeij 1987, 1993, 1977*a*, 1982*a*; Palmer 1979; Vermeij et al. 1980; Menge and Sutherland 1987; Behrens Yamada and Boulding 1996; Bertness et al. 2004; Schemske et al. 2009). In both modern ecological and palaeontological studies, predation traces are often the only source of information to indicate or quantify interactions between predators and prey, particularly if predators are more difficult to find or observe. For example, crab predation scars on gastropods have been used to assess patterns as broad as the development of antipredatory adaptations and gastropod diversity (Vermeij 1977*a*, 1982*b*, 1993; Vermeij et al. 1981; Alexander and Dietl 2003), and as local as variation in predation rates in modern ecosystems (Schmidt 1989; Schindler et al. 1994; Cadée et al. 1997; Dietl and Alexander 1998, 2009; Alexander and Dietl 2001; Molinaro et al. 2014; Stafford et al. 2015*a*). From a modern conservation perspective, predation traces can provide useful information on how crabs and their ecosystems might be affected by environmental disturbances, and can be used to assess crab predation dynamics when either recent, historical, or fossil records of crabs are sparse (Tyler et al. 2019). Here we examine crab predation scars on a common and widespread crab prey item, the black turban snail (*Tegula funebralis*), from both Late Pleistocene and modern, living populations of southern California. By comparing predation patterns in fossil and modern populations, we aim to identify potential evolutionary patterns between predators and prey, and determine whether repair scars may be useful in examining crab population health and quality when access to crab data is limited.

In marine systems, predators are well-known to regulate prey populations and their distributions (e.g., Paine 1966, 1969*a*; Menge and Sutherland 1987; Bertness et al. 2004). For example, both sea stars and crabs are known to control the distribution of prey species, including mussels and snails within rocky intertidal habitats along the west coast of North America (Paine 1969*b*; Markowitz 1980; Fawcett 1984; Behrens Yamada and Boulding 1996; Dietl and Alexander 2009; Gravem and Morgan 2017; Hull and Bourdeau 2017). Not only can predators potentially control prey population sizes and/or their distributions, but the presence of predators can also exert selective pressure on their prey both directly and indirectly (Trussell et al. 2003). Unsuccessful predation produces selective pressure in that traits which allow prey to survive an attack may lead to increased reproductive potential of those individuals (Vermeij 1982*a*). Even without direct attacks, the presence of predators and predatory activities may elicit fear responses in prey which affect their foraging and growth (Appleton and Palmer 1988; Palmer 1990; Marko and Palmer 1991; Trussell et al. 2003; Jacobsen and Stabell 2004; Mach and Bourdeau 2011). The ability to quantify the intensity of predation is therefore essential in understanding how predation regulates prey populations and their characteristics, especially over evolutionary time scales.

Traces of shell-crushing (durophagous) predation have been widely used in both modern ecological and palaeontological studies to quantify predation intensity (Vermeij 1977*a*, 1982*b*, 1983, 1987; Zipser and Vermeij 1978; Vermeij et al. 1980, 1981; Schindel et al. 1982; Geller 1983; Schmidt 1989; Cadée et al. 1997; Dietl and Alexander 1998, 2009; Alexander and Dietl

2001, 2003; Leighton 2011, 2002; Dietl et al. 2010; Stafford and Leighton 2011; Richards and Leighton 2012; Leighton et al. 2013; Dietl and Kosloski 2013; Molinaro et al. 2014; Mondal et al. 2014*a*, *b*; Mondal and Harries 2015; Stafford et al. 2015*a*; Harper and Peck 2016; Pruden et al. 2018; Tyler et al. 2019) Successful shell-crushing predation attempts usually result in the destruction of the shell and leave little evidence (Stafford and Leighton 2011; Pruden et al. 2018), but see Leighton et al. (2016). Instead, measures of predation intensity are limited to unsuccessful predation attempts, traces usually referred to as repair scars. In most cases, predation intensity is inferred from the frequency of repair scars traces observed in a population, using either or both the number of individuals which are scarred, and the total number of scars (Vermeij et al. 1980, 1981; Vermeij 1982*b*, 1993; Schindel et al. 1982; Geller 1983; Schmidt 1989; Dietl and Alexander 1998; Alexander and Dietl 2001, 2003; Leighton 2002; Molinaro et al. 2014; Mondal et al. 2014*a*; Mondal and Harries 2015; Pruden et al. 2018; Tyler et al. 2019). In modern studies, repair frequency has been found to reflect predator abundance and/or the number of attacks accurately (Schindler et al. 1994; Molinaro et al. 2014; Stafford et al. 2015*a*). However, there is some ambiguity when comparing repair frequency between assemblages, particularly those separated temporally, as failed attacks may also reflect the success rates of predators (Vermeij 1987; Leighton 2002; Alexander and Dietl 2003). For example, a reduction in repair frequency through time or space can indicate one of two results: it might simply reflect a reduction in attack frequency, but if attack rate was held constant, the same result might be produced if predators became more successful against their prey. The ability to assess success of predators using additional or alternative metrics therefore becomes critical to accurate interpretation of repair frequency. One such method is to measure the size at which repairs (failed attacks) occur on prey.

Assuming prey size is held constant, if the distribution of repair size increases, such that larger prey have repair scars, this suggests that the predators have become stronger and therefore more successful relative to their prey. Presumably, an increase in predator strength would also involve fewer repairs on smaller individuals, as it would be easier for stronger predators to crush smaller gastropods, leading to fewer failed attacks (repairs) on gastropods of that size. Therefore, a shift in the distribution of repairs towards larger prey indicates more successful predators that are not only capable of attacking large prey, but also presumably fail less often on smaller prey (Leighton 2002; Richards and Leighton 2012; Pruden et al. 2018, Barclay and Leighton, in prep.). If repair frequency was also found to decrease over time in conjunction with an increase in repair sizes, it likely signals that reductions in repair frequency are due to increased predator success (the predators are less likely to fail). Alternatively, if repair frequency changed, but the size of repairs remained the same, there is nothing to suggest that predator success has changed, which most likely indicates that there was a change in the number of attacks.

However, even if success increases, if the addition of more repairs at larger sizes is proportional to the loss of repairs at smaller sizes, the overall number of repairs observed might not change, thus repair frequency may not be affected (e.g., Fig. 5.3C). The same would be true if predator success decreased, with more smaller repairs because the predator failed more often, but proportionately fewer repairs at large sizes because the predators could not attack that prey size (e.g., Alexander and Dietl 2001; Mondal et al. 2014*a*) (e.g., Fig. 5.3B). Repair frequency should only be affected in circumstances in which the relative distribution of repairs changes in relation to the distribution of prey available to the predator. Even if prey size changed, the observed number of failures might not be affected if there is a corresponding change in the size of repair scars (e.g., Fig. 5.3D, E). In other words, regardless of changes in the strength of the predator (size of prey attacked), if the change in size of repairs remains relative to a change in the size of the prey, repair frequency (the observed number of failures) may not be affected because predator success/strength has remained relative to the prey available to them. Instead, repair frequency might only be affected if the distribution or observed range of repairs changes relative to range of prey sizes. For example, if the maximum repair size increased, but there was an even greater increase in the minimum size of repair (i.e., the addition of repairs at larger sizes is less than the loss of repairs at smaller sizes), it might indicate that the observed repairs would be lower than expected compared to a sample in which the distribution of repairs remained relative (e.g., Fig. 5.3H). In this example, success not only increased in terms of the maximum size of repair, but there was a disproportionate loss of small repairs (presumably because predators were less likely to fail in that size range) that would likely lower the number of repairs observed. Alternatively, if the minimum size of repairs decreased relative to the prey size (relatively more repairs at smaller sizes), repair frequency may be greater than expected because there is a larger range/distribution of failed attacks (e.g., Fig. 5.3F). It is therefore possible that success can be measured independently of repair frequency, with repair frequency (observed failures) only being affected if the relative success is different among samples. Here, we use the size of repairs relative to overall prey size as a means of testing this potential relationship between success, observed failures (repair frequency), and prey size.

One of the best studied repair scar systems is that of crab predation traces on gastropods (Vermeij et al. 1980, 1981; Vermeij 1982*b*; Schindel et al. 1982; Geller 1983; Schmidt 1989; Schindler et al. 1994; Cadée et al. 1997; Dietl and Alexander 1998, 2009; Alexander and Dietl 2003; Dietl and Kosloski 2013; Molinaro et al. 2014; Stafford et al. 2015*a*; Tyler et al. 2019). When a crab attacks a gastropod, it attempts to crush the shell, but if it is unable to do so, it will switch to a method called "peeling" wherein the crab inserts its dactyl(s) into the apertural opening and attempts to break off pieces of the apertural lip (Zipser and Vermeij 1978). If unsuccessful, these peeling traces produce distinct scars on the gastropod's shell in the form of a distinct wedge-shape on the whorl which intersects growth lines, identified as the ichnotaxon *Caedichnus* (Stafford et al. 2015*b*) (Fig. 5.1A). As these attacks occur at the aperture, and gastropods grow by accretion, the shells of gastropods record not only the number of predation attempts experienced over the course of their lifetime, but also the size of the gastropod at the time of each attack. By measuring the size of these repairs and comparing them between populations or assemblages, patterns of relative crab success may be determined.

Along the west coast of North America, cancrid rock crabs, such as *Cancer productus*, *Romaleon antennarium*, and *Metacarcinus anthonyi*, are important shell-crushing predators that contribute to the regulation of rocky intertidal ecosystems (Behrens Yamada and Boulding 1996; Hull and Bourdeau 2017). Rock crabs are a small fishery compared to larger and more profitable Dungeness crabs, but the rock crab fishery has become more economically important and grown substantially in recent years (Fitzgerald et al. 2018). However, management of the fishery is hampered by a lack of data other than gross landings (Culver et al. 2010). In California, permit numbers are restricted, and a catch size limit is in place, but as there are multiple, differently sized species of rock crabs, and abundance varies spatially, the effectiveness of these restrictions is unknown, and evidence suggests overfishing is likely already affecting rock crab body and population sizes (Fitzgerald et al. 2018, and references therein). As current data on rock crabs are lacking and difficult to obtain, the use of crab predation traces on their prey might offer critical insights on crab population health which can help guide management decisions.

To make any inferences about crab population health or current trends in crab predation requires the establishment of a baseline by which to compare current conditions. The same is true if we wish to understand long term evolutionary changes to predator-prey systems. As historical records of rock crabs are sparse, examining historical and palaeontological collections of prey items offer insights into long-term records of crab predation. However, as there has been rapid development and urbanization along the coast of southern California in the last 70 or more years (Woodring et al. 1946; Whitaker et al. 2010), historical collections may already be biased by human activity (Rick et al. 2014). Furthermore, humans have been active in southern California for at least the past 12 – 13,000 years (Rick et al. 2014; Erlandson et al. 2015), where they have harvested and influenced population and body sizes of common crab prey items, such as abalone, and turban snails (Erlandson et al. 2015). Therefore, older fossil material from interglacial highstands similar in climate to the present may be considered more conservative, or unbiased "baseline" populations.

During the Last Interglacial Complex (LIC), a combination of uplift and fluctuating sea-level led to the development of a series of step-down fossiliferous marine terraces along the coast of southern California (Woodring et al. 1946; Valentine 1962; Kern 1977; Muhs et al. 1994, 2012, 2014). Older terraces are found at higher elevations, with each lower terrace being subsequently younger (Woodring et al. 1946; Valentine 1962; Kern 1977; Muhs et al. 2006). In the Palos Verdes Hills area near Los Angeles, there have been upwards of twelve terraces identified (Woodring et al. 1946), with the lower terraces representing oxygen isotope substages 5e (~120,000 ya) and 5a (~80,000 yr BP) (Muhs et al. 2006). In the San Diego area, there are two similarly aged terraces present: the Nestor Terrace (~120,000 ya, but also possibly mixing from ~100,000 ya), and the younger Bird Rock Terrace (~80,000 ya) (Kern 1977; Kennedy et al. 1982; Muhs et al. 1994, 2012).

There has been a considerable amount of work trying to determine palaeotemperatures during these high stands with much of the work on molluscs based on comparing fossil faunal assemblages to their present zoogeographic ranges and identifying whether fossil assemblages contain either northern or southern species that would indicate either warmer or cooler waters (Woodring et al. 1946; Valentine 1962; Roy et al. 1995; Muhs et al. 2014). However, most of the assemblages contain “thermally anomalous fauna” that have complicated interpretation of palaeotemperatures (Valentine 1962; Roy et al. 1995; Muhs et al. 2014). Instead, as marine oxygen isotope substages (MIS) have been well established, the focus has been on accurate age dating of the fossil assemblages (e.g., Uranium-series and aminostratigraphy) to link them to the appropriate MIS precisely (Kennedy et al. 1982; Muhs and Kyser 1987; Muhs et al. 1994, 2006, 2012, 2014). The most recent research suggests that the older terraces (~120,000 ya) had a similar temperature and climate to that of today, whereas the younger terraces (~80,000 ya) were likely cooler than today (Muhs et al. 2006, 2014).

The black turban snail, *Tegula funebralis* (Adams 1855), is an abundant grazer found in most rocky intertidal communities from Alaska to Baja California (Frank 1975). The species first appears in the Pliocene (Hellberg 1998), and while the fossil record of *T. funebralis* is patchy, as is typical with most intertidal fauna (Walker and Carlton 1995), it is present in some of the lower Late Pleistocene marine terraces of southern California (Valentine 1962; Walker and Carlton 1995). Crab predation on *T. funebralis* has been well studied both in the lab (Geller 1982*b*; Jacobsen and Stabell 2004; Mendonca et al. 2017), as well as from repair scar surveys of natural populations (Geller 1983; Molinaro et al. 2014; Stafford et al. 2015*a*; Tyler et al. 2019, Barclay and Leighton, in prep.)(Molinaro et al. 2014; Stafford et al. 2015*a*; Tyler et al. 2019). Repair scars on modern *T. funebralis* populations suggest that repair frequency is an accurate proxy for attack frequency and crab abundance throughout most of its range (Molinaro et al. 2014; Stafford et al. 2015*a*, Barclay and Leighton, in prep.). However, crab predation in Pleistocene *T. funebralis* has never been examined. It is therefore unknown how crab predation on *T. funebralis* has developed over the past 120,000 years.

Cancrid crabs are important shell-crushing predators along the west coast of North America, where they are not only well-known consumers of *T. funebralis* (Geller 1982*b*, 1983; Molinaro et al. 2014; Stafford et al. 2015*a*), but can also act as keystone predators that exert both direct and indirect control over their ecosystems (Hull and Bourdeau 2017). Cancrids from the Pleistocene of southern California are known mostly from chela (claws), which preserve more readily (Menzies 1951; Nations 1975). Pleistocene species and their distributions are comparable to the present, consisting of the same major cancrid taxa, including *Cancer productus, Metacarcinus anthonyi*, *M. gracilis*, *M. magister*, *Romaleon antennarium*, and *R. branneri* (Menzies 1951; Nations 1975). The only notable difference is the presence of *Glebocarcinus oregonensis* (the pygmy rock crab) in the Pleistocene of southern California, which does not extend south of Santa Barbara today (Nations 1975). Given that the shell-crushing crab taxa are similar between the Pleistocene and modern, and that repair scars do not allow differentiation between species of cancrid crabs, it is reasonable to assume that repair scars themselves should appear similar between the Pleistocene and modern of southern California, and therefore allow a comparison of repair scar frequency and success.

In the following study, we compare patterns of crab predation on a common and widespread gastropod, *T. funebralis*, between the Late Pleistocene and today. We measure prey body size and compare both the frequency of repair scars and size at which repair scars occur as a means of assessing the strength and relative success of Pleistocene and modern crabs. Our goals were to determine: 1) how gastropods and repair scars have changed over evolutionary time scales, and 2) how the fossil record of predation might provide context and insights on the current health of crab populations that could help guide fishery management decisions.

6.2 Methods

6.2.1 Fossil Material

Fossil *T. funebralis* material came from the Natural History Museum of Los Angeles County invertebrate paleontology (LACMIP) collections. Any lot containing *T. funebralis* was assessed, and of those, all adult *T. funebralis* (those containing at least 3 body whorls) that were "intact" (minimally a complete apex and aperture, and no more than 25% of any whorl missing) were measured and assessed for repair scars. The bulk of southern California *T. funebralis* material in the collections came from the lower terraces of the Palos Verdes Hills and San Pedro area (as identified by comparing lot GPS coordinates with terrace maps (Fig. 6) from Muhs et al.

(2006) if the exact terrace was not specified), and from terraces from the San Diego area (Fig. 6.1). We therefore restricted ourselves to including only specimens from those areas and terraces in subsequent analyses. As some of the lots lacked specific terrace information, or stated that they were taken from multiple terraces at one locality, we conservatively assumed that there was at least some mixing of the 120 ka and 80 ka terraces in both areas. We therefore treat all fossil material as a potentially time averaged “Late Pleistocene” assemblage, representing up to approximately 40,000 years of time, but still separated from the modern material by about 80,000 years. Therefore, any biological signals that were apparent despite potential time averaging of the Pleistocene material were assumed to be robust. We had a total of 712 fossil specimens (261 from the Palos Verdes Hills area, and 451 from the San Diego area).

6.2.2 Modern Specimens

Live specimens of *T. funebralis* were measured *in situ* at seven localities (four from the Palos Verdes Hills area near Los Angeles, and three from the Bird Rock area north of San Diego) in the early morning during the first low tide cycle of July 2019 (Fig. 6.1). The two study areas were selected based on their proximity to the areas where the fossil material had been collected, and all rocky intertidal outcrops in those areas that were publicly accessible were surveyed for *T. funebralis.* Any site which contained *T. funebralis* was surveyed, with the exception of a single site of abundant *T. funebralis* near San Pedro (Point Fermin Park) which became inaccessible due to several earthquakes that occurred during the survey period and caused instability of the cliffs above the site. The seven sites are therefore representative of the range of moderately wave-exposed and cobbled, rocky shore habitats typical of *T. funebralis* in southern California. At each site, approximately 150 averaged-sized adults (those that had at least three body whorls) were collected for measuring. Collection was spread out over the entire site to ensure there were no biases due to spatial or tidal/vertical positions of the snails. Specimens were measured, and then quickly returned to their approximate location to ensure minimal disturbance before the tidewaters returned. We measured a total of 1152 modern specimens across the seven sites.

6.2.3 Data Collection

In both the fossil collections and modern sites, gastropods containing fewer than three whorls were avoided, as individuals within those size ranges are more likely to be successfully crushed by crabs, and therefore likely have few repairs (Molinaro et al. 2014). Each specimen was assessed for repair scars, and measurements of size were taken (both maximum height and width). If a scar was present, an additional measurement, the size at attack (referred to as SAA) was also taken. As repair scars are formed when a crab attempts to peel back the aperture, and gastropods grow their shells by accretion, the SAA measurement indicates the width of the animal at the time it was attacked. SAA was measured from the point at which the repair met the top of the whorl along a line segment passing through the apex to the point on the opposite side of the gastropod (Fig. 5.1B). If a gastropod had more than one repair, the SAA was measured for each, as they indicated separate attack events.

6.2.3 Analyses

To determine if 1) the presence or number of scars on each gastropod, 2) size, or 3) SAA, differed between the Pleistocene and the modern, we ran a series of Wilcoxon rank sum tests (non-parametric equivalent of a t-test) on each. We then tested if the presence or number of scars were also affected by size by fitting generalized mixed models to scars. As each gastropod could have multiple SAA measurements, the SAA dataset was independent of measures from the individual gastropod (such as size or the number of scars) and was therefore not added to models of repair scars. The presence or number of scars on each gastropod was the dependent (response) variable, with size and time as independent (fixed) variables. Region (Palos Verdes versus San Diego) was also included as an independent variable to ensure that region was not affecting the results. Lot/locality was included as a random effect. For presence/absence of scars, specimens were coded as scarred (1) or unscarred (0), and a binomial family link was used to fit the model. To test which independent variables affected the total number of scars on each specimen, a Poisson family link was used to fit the model, in which the number of scars was treated as discrete/count data. The best model was determined by comparison of the Akaike Information Criterion (AIC) scores, where the lowest score indicated the best model. We used log-likelihood ratio tests to determine if the best fitted model performed significantly better than a null model (which only included lot/locality as a random effect, and no independent variables). Significance of the independent variables on predicting scars was then examined using Wald Z-scores. If both size and time (Pleistocene vs. modern) were found to have significant effects on the presence or number of scars, we then assessed the strength/direction of the relationship between scars and size by running a partial correlation where we backed out the effects of time. All analyses were performed with R (version 3.4.4) using the lme4 package.

As mentioned, given that a single gastropod could have more than one scar, and therefore multiple SAA measurements per specimen, the SAA dataset was independent and not comparable to number of scars or size data for regression analyses. Instead, SAA was used to gauge potential differences in the success of crabs, both in terms of the strength of crabs and relative distribution of repairs sizes compared to the distribution of prey sizes, and the potential consequences for the number of failures/repair frequencies observed between the two time periods. Previous work has suggested that even if the success/size of prey that a crab can kill changes between assemblages, repair frequency might not change if there is also a relative change in the size of the prey (Barclay and Leighton, in prep) (e.g., Fig. 5.3). In other words, if the distribution of repairs remains the same relative to the distribution of prey size, we would not expect to see a difference in the observed number of repairs, and therefore any changes in repair frequency likely indicate a change in the number of attacks experienced. We compared crab strength (size of repairs) via the Wilcoxon rank sum test of SAA. Relative success between the Pleistocene and modern was compared by plotting histograms of SAA and gastropod size (width) to determine whether there were any obvious differences in the relative distributions of both. Specifically, we measured: [1] the distance between minimum SAA and width, [2] the proportion of repairs occurring below the minimum size of the gastropods, [3] the proportion of repairs occurring between the minimum and median gastropod size, and [4] the distance between the maximum SAA and width (Fig. 5.3A). The distance between the minimum SAA and gastropod size [1], as well as the distance between the maximum SAA and gastropod size [4], can be used to capture the relative range of observed repair sizes between samples to ensure that repair frequencies are comparable, particularly against the largest and smallest gastropods where SAA is most likely to shift between samples (Fig. 5.3A). If one sample has a narrower range of repair sizes compared to another, it may indicate that repair frequencies in that sample will be lower than expected, and vice versa (Fig. 5.3H, I, K). The proportion of attacks below the minimum gastropod size [2] and between the minimum and mean gastropod size [3] can be used to compare relative success between samples (i.e., are most of the repairs on larger or smaller gastropods at that site?) (Fig. 5.3).

6.3 Results

Pleistocene gastropods had more scars than modern gastropods ($p < 0.0001$) (Table 6.1, Fig. 6.2C). Modern gastropods were also significantly larger, as were modern repair sizes (SAA) ($p<0.0001$) (Table 6.1, Fig. 6.2A, B). As there was, unsurprisingly, a very strong correlation between height and width ($R = 0.953$, $p < 0.0001$), we used width measurements as our size variable in all models. The best model of repairs included both time and size, with both time and size having significant effects on scars (Table 6.2). Size had a significant effect on whether a gastropod had one or more scars, with scarred gastropods being slightly larger than unscarred gastropods (Table 6.2, Fig. 6.2C). However, the effects of size appeared relative to each assemblage, as time still had a significant effect on whether a gastropod had at least one scar, with individual Pleistocene gastropods being more likely to have scars (Table 6.2). When backing out the effects of time, the presence and number of scars showed a weak, but significant correlation with size (partial $R = 0.132$ and 0.139, respectively, $p < 0.0001$). Region (Palos Verdes vs. San Diego) did not have a significant effect on scars or model performance (Table 6.2).

Crab strength (SAA) of modern crabs was greater, as indicated by larger SAA sizes in the modern ($p < 0.0001$). While we were not able to test for significance of relative success (there were only two data points to compare), we could make some observations on relative success based on the distributions of SAA versus gastropod size (width) for the two time periods. First, the distance between the minimum SAA and the minimum gastropod size [1] was almost twice as large in the modern compared to the Pleistocene (8.12 mm vs. 4.86 mm) (Fig. 6.3). Furthermore, there were three times more repairs that occurred below the minimum gastropod size [2] in the modern (12.7% vs 4.3%) (Fig. 6.3). However, between the Pleistocene and modern, both the proportion of repairs that occurred between the minimum and mean gastropod size [3] (57.1 and 59.4 %, respectively), and the distance between the maximum SAA and maximum gastropod size [4] (2.50 vs 3.09 mm, respectively) were similar (Fig. 6.3).

6.4 Discussion

The current lack of detailed information on rock crabs in southern California presents a similar problem to what is often observed in the fossil record where the preservation, or access, to crab prey items, such as gastropods, is far better than to the predators themselves. By examining the common prey item *T. funebralis* and their crab repair scars between similar environments from the Late Pleistocene and today, we were are able to compare patterns of repair scars and find evidence that crabs and snails may have responded to one another since the Late Pleistocene. While modern gastropods are larger and were repaired at larger sizes (indicating that modern crabs are stronger and more successful in terms of the size of prey they fail against), there were comparatively more repairs on relatively small gastropods in the modern than in the Pleistocene (Fig. 6.3), suggesting that if anything, Pleistocene crabs were relatively more successful (less likely to fail) against the gastropods available to them (at least for relatively small gastropods) (e.g., Fig. 5.3H). As such, we would have expected the potential number of observed repairs to be comparatively lower in the Pleistocene (relatively fewer failures on small gastropods). Instead, we found that modern gastropods are less likely to have repairs (Fig. 6.3B), suggesting that attack frequencies are lower today than they were in the Pleistocene. We offer several alternative explanations to explain the possible reductions in modern crab attacks, all of which suggest that further study of modern crab populations is needed. Repair scars are therefore a useful metric for assessing crab predation when comparing modern and fossil data and can provide useful information that may help guide management or further lines of inquiry for rock crab fisheries.

6.4.1 Patterns in Predation

Along the southern California coast, we find that modern *T. funebralis* 1) have fewer scars, 2) are larger than their Pleistocene counterparts, and 3) are repaired at larger sizes. As modern gastropods were repaired at larger sizes, the strength (SAA) of crabs has increased since the Pleistocene. However, as the size of gastropods also increases, the loss of smaller repairs is offset by the addition of larger repairs, suggesting that the number of repairs expected should be similar between the two samples (e.g., Fig. 5.3B vs. D). The success of the crabs against the gastropods available to them in either sample can instead be assessed by comparing the relative distribution of repairs to the distribution of gastropods available to the crabs. For example, even if gastropod size did not overlap between samples, if the observed repairs show the same distribution relative to the gastropods, the relative success of crabs against those two gastropod populations would be the same. Therefore, any changes to repair frequencies are most likely the result of a change in attack rates. This scenario appears to be true for our dataset (Fig. 6.3), even though crab strength (SAA) has increased since the Pleistocene (e.g., Fig. 5.3B vs. D, C. vs. E). If anything, Pleistocene crabs were relatively more successful against the gastropods available to them, as there were comparatively few repairs at relatively small sizes in the Pleistocene compared to today (Pleistocene crabs failed less often on small gastropods) (Fig. 6.3). Fewer repairs in the modern is therefore most likely an indication of fewer attacks, rather than a change in success, as while strength (SAA) of modern crabs is greater, the relative success of modern crabs, if anything, is slightly reduced (Fig. 6.3B). Given that under these circumstances we would have expected fewer scars if Pleistocene crabs were relatively more successful and less likely to fail compared to modern crabs, the finding of fewer observed repairs on modern gastropods can conservatively be interpreted as indicating fewer attacks on modern gastropods. We present several alternative hypotheses to explain both the reduction in modern crab attacks, along with increases in body size and SAA. At minimum, all indicate that further investigation of crab populations and ecosystem health is highly warranted.

With respect to fewer attacks on modern gastropods, it is possible that crabs have switched to other prey items, and *T. funebralis* are attacked less often. For example, mussels are a preferred prey item of crabs that are easier to kill than *T. funebralis* (Leighton and Tyler in review), and it is conceivable that mussels would be attacked more often. However, we did not observe any large mussel beds at any of the modern sites, and there have also been notable declines in mussel populations in southern California in recent decades (Smith et al. 2006). In addition, *T. funebralis* in southern California show lower repair rates than other areas along the west coast of North America (Barclay and Leighton, in prep.), including sites which still contain abundant mussel beds (pers obs.). This suggests that if anything, a reduction in mussel populations in present-day southern California might increase crab predation on *T. funebralis*, yet we observe the opposite. While there are other prey items which might also be preferred, such as owl limpets and other species of *Tegula*, including *T. brunnea* and *T. eiseni*, which both have lower tidal ranges (and would therefore spend more time exposed to crabs), these species were also present during the Late Pleistocene. It therefore seems unlikely that prey-switching alone would cause such reductions in modern repair scars on *T. funebralis.*

A more likely possibility is that modern crabs have become more restricted vertically, either due to stress or habitat loss, and do not have as many opportunities to feed on *T. funebralis* in its given tidal range. Along with the recent declines in mussel populations, rockweeds and larger habitat forming macroalgae have also declined in southern California in recent years (Whitaker et al. 2010; Jurgens and Gaylord 2018). Indeed, at most of our sites, there was a lack of rockweeds and other large macroalgae, with *T. funebralis* found most commonly on bare rock covered in biofilm (pers obs.). The loss of rockweed and habitat forming macroalgae may therefore be critical to crabs, as habitat forming species are critical buffers against temperature stress, and often provide more control than latitude or tidal elevation (Jurgens and Gaylord 2018). Crabs are also nocturnal predators, typically hiding from their own predators amongst cobbles and macroalgae, particularly when they are younger (Robles et al. 1989; Behrens Yamada and Boulding 1996; Behrens Yamada and Groth 2016). The loss of cover may therefore restrict crabs to foraging mostly at lower tidal heights where there is still more abundant macroalgae, which might not have been the case until recently.

Another equally troubling reason for the decline in crab predation on modern *T. funebralis* in southern California could be a reduction in the abundance of crabs. Again, not only are there fewer repairs on modern *T. funebralis* compared to their Late Pleistocene counterparts, but southern California *T. funebralis* are also attacked less often than other regions along the west coast of North America (Barclay and Leighton, in prep.). Crab fisheries in California have grown substantially since the 1980s, and there have been concerns about the lack of data to guide crab fisheries management (Culver et al. 2010). Recent studies have noted concerns from fishermen and researchers about observed changes to crab body size and abundance in southern California, while also providing data modelling which suggests early warning signs of crab overfishing in southern California (Fitzgerald et al. 2018). Our results support a potential decrease in rock crab abundances in southern California, suggesting that repair scars may be a critical tool for monitoring crab population health in crab fisheries worldwide.

It is also possible that a difference in in temperature, particularly since the cooler 80,000 ya highstand, might therefore have affected predation rates, and/or caused a change in both the size of *T. funebralis* and their crab predators. However, as there was potential mixing of two highstands, or about 40,000 years, including the lots from the Palos Verdes Hills area that were likely attributed to the older 120,000 ya highstand which was similar in temperature to today, temperature alone is likely an insufficient explanation for changes in body and repair sizes. Furthermore, as increases in temperature also increase predation rates (Leighton and Tyler in review), and the relative success of the crabs, if anything, has decreased compared to the Pleistocene, we would have also expected more repair scars at modern sites, yet the opposite is true. Archaeological studies of *T. funebralis* size over the last 12,000 years have found that *T. funebralis* body size was not correlated with temperature (SST), and instead was influenced by human predation intensity (Erlandson et al. 2015). It therefore seems more likely that *T. funebralis* size is influenced by predation rather than temperature.

6.4.2 Patterns in Gastropod Size

Beyond predation rates, there are two alternative explanations for larger *T. funebralis* body size in the modern compared to the Pleistocene, if we assume that temperature is not driving patterns in *T. funebralis* body size or predation. First, it is possible that we are seeing evidence of an “arms-race” between *T. funebralis* and their crab predators. Crab predation could be acting as a selective pressure for larger body size in *T. funebralis* populations. SAA is also larger today than in the Pleistocene, indicating that modern crabs are capable of attacking larger gastropods, and may have increased in size and strength. Modern *T. funebralis* in Oregon show a similar pattern, where body size is much larger than elsewhere along the west coast of North America, as are repair sizes (Barclay and Leighton, in prep.). However, as relative success might be greater in the Pleistocene (there are fewer repairs on small gastropods) compared to today, modern gastropods may be “winning” the arms-race in that modern crabs are more likely to fail than their Pleistocene counterparts, at least on relatively small gastropods. Selective pressures from one’s own predators should be stronger than the selective pressure to catch prey (Vermeij 1987), which suggests that *T. funebralis* have likely experienced greater selective pressures compared to their crab predators. As crabs might be expected to respond more strongly to their own predators (Vermeij 1987), and these cancrid crabs are generalists that feed on many different prey, selective pressures to crush *T. funebralis* are likely not as strong as the selective pressure to avoid shell-crushing predation experienced by *T. funebralis*.

A second possibility to explain increased *T. funebralis* body size, assuming temperature is not having an effect, is that because there are fewer attacks today compared to the Pleistocene, more snails today are surviving and growing to larger sizes. As is the case with most sources of predation on prey populations, human harvesting of *T. funebralis* in archaeological records is known to have negative effects on body size (Erlandson et al. 2015). It is therefore possible that other predators, such as crabs, might also exert some control over *T. funebralis* body size. A decrease in crab predation might therefore be associated with increases in *T. funebralis* body size. Additionally, sea stars are another major predator of *T. funebralis* (Paine 1969*b*; Markowitz 1980; Fawcett 1984; Gravem and Morgan 2017), and sea stars populations have been severely affected by an outbreak of sea star wasting disease in 2013 (Hewson et al. 2014; Menge et al. 2016). Reductions in predation on modern *T. funebralis* from either crabs or sea stars could also explain their larger body sizes compared to Pleistocene *T. funebralis.*

Regardless of the cause(s) for changes to predation rates, body size, or SAA, the use of crab predation traces provides abundant, easily accessible data where it might otherwise be challenging to gather data from the crabs themselves, particularly if current or historical records are sparse or lacking. Fossil data can also provide a baseline that can be used to assess changes to both gastropods and their crab predators that are well outside of any potential consequences of either human presence or modern industrialization. Our results suggest that there have been reductions in the amount of predation experienced by modern gastropods, most likely caused by human-induced changes. Repair scars are therefore an essential indicator or “canary in the coal mine” that can be used to assess whether further action is needed to gather data and provide greater protections for potentially vulnerable populations of crabs.

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Table 6.1

Wilcoxon rank sum tests of Pleistocene vs. modern repair scars, size, and SAA. Comparisons of scars were conducted as both the presence/absence of a scar (scars/no scars), and the number of scars. Width (mm) was used for comparisons of size.

	W	p-value
Scars/no scars	378420	**<0.0001**
number of scars	378260	**<0.0001**
Width	540520	**<0.0001**
SAA	41910	**<0.0001**

Table 6.2

Mixed models of the presence/absence of a scar (binomial family, link = logit, scarred = 1, unscarred = 0), and the number of scars (Poisson family for count data, link = log). Fixed effects = time (modern vs. Pleistocene), size (gastropod width), and region (Palos Verdes vs. San Diego areas). Random effect = lot/locality. Performance of the models for each dependent variable (unscarred/scarred or number of scars) was compared using log-likelihood ratio tests of a null (intercept and random effects only) vs. full model including all fixed effects (time, size, and region). Significance of the fixed effects was assessed Wald Z-test scores.

Scarred/unscarred models (family = binomial (link=logit))								
Model	**AIC**	**BIC**	**logLik**	**Resid. Df**	**Resid. Dev**	**Chisq**	**Chi DF**	**Pr(>Chi)**
Null	1972.0	1983.0	-984.0	1863	1968.0			
Full (Time + Size + Region)	**1945.0**	**1972.7**	**-967.5**	**1935**	**1860.0**	**32.953**	**3**	**<0.0001**
				Random effects		**Name**	**Variance**	**Std. Dev**
				Lot/Locality		(Intercept)	0.1605	0.4006
			Fixed effects		**Estimate**	**Std. Error**	**z value**	**Pr (>|z|)**
			Intercept		-3.4639	0.4259	-8.1340	**<0.0001**
			Modern vs. Pleistocene		0.7326	0.2285	3.2060	**0.0014**
			Width		0.0918	0.0182	5.0570	**<0.0001**
			Region		0.1243	0.2244	0.5540	0.5798
Number of scars models (family = Poisson (link = log))								
Null	2425.1	2463.1	-1210.5	1863	2421.1			
Full (Time + Size + Region)	**2394.8**	**2422.5**	**-1192.4**	**1860**	**2384.8**	**36.256**	**3**	**<0.0001**
				Random effects		**Name**	**Variance**	**Std. Dev**
				Lot/Locality		(Intercept)	0.1205	0.3471
			Fixed effects		**Estimate**	**Std. Error**	**z value**	**Pr (>|z|)**
			Intercept		-3.2162	0.3370	-9.5430	**<0.0001**
			Modern vs. Pleistocene		0.5618	0.1897	2.9620	**0.0031**
			Width		0.0745	0.0139	5.3580	**<0.0001**
			Region		0.2337	0.1846	1.2660	0.2056

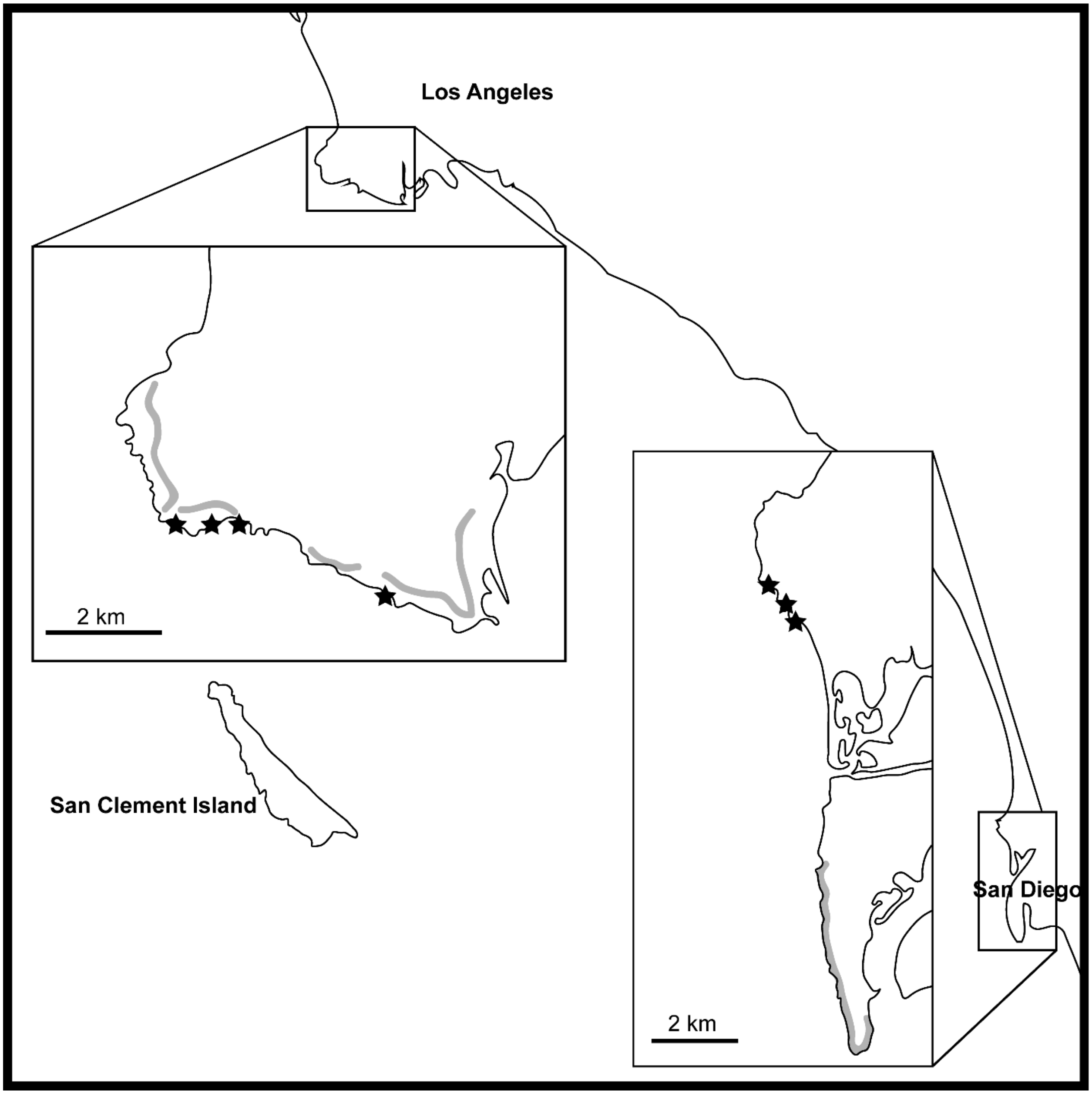

Figure 6.1

Map of southern California between Los Angeles and San Diego. Map insets show the two study areas (Palos Verdes Hills and San Diego) in more detail. Modern localities are indicated in black stars (four from the Palos Verdes Hills area, and three from north of San Diego). Approximate fossil localities are indicated by grey shaded lines which indicate the terraces and/or GPS coordinate information that accompanied fossil lots. Terraces in the Palos Verdes Hills are based on Fig. 6 of Muhs et al. (2006). Scale bar in each inset is 12 kms.

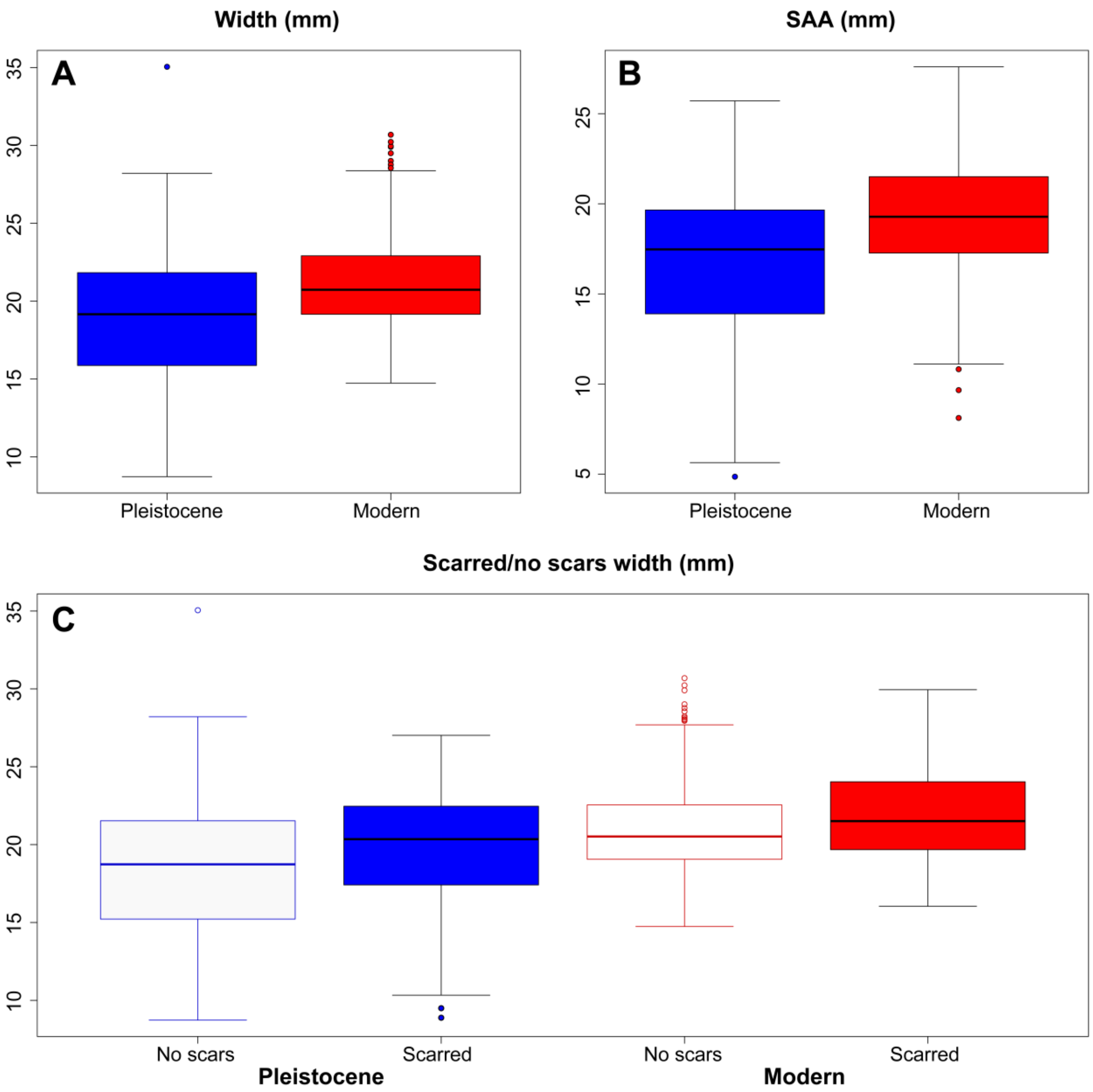

Figure 6.2

Boxplots showing differences in gastropod body size, size at attack (SAA), and the size (width) of scarred vs. unscarred individuals between Pleistocene and modern samples. A. Gastropod size (width). **B.** SAA. **C.** Differences in the size of unscarred and scarred gastropods for both Pleistocene and modern samples. Boxes = upper and lower quartiles, central lines = medians, whiskers = min/max data, circles = outliers.

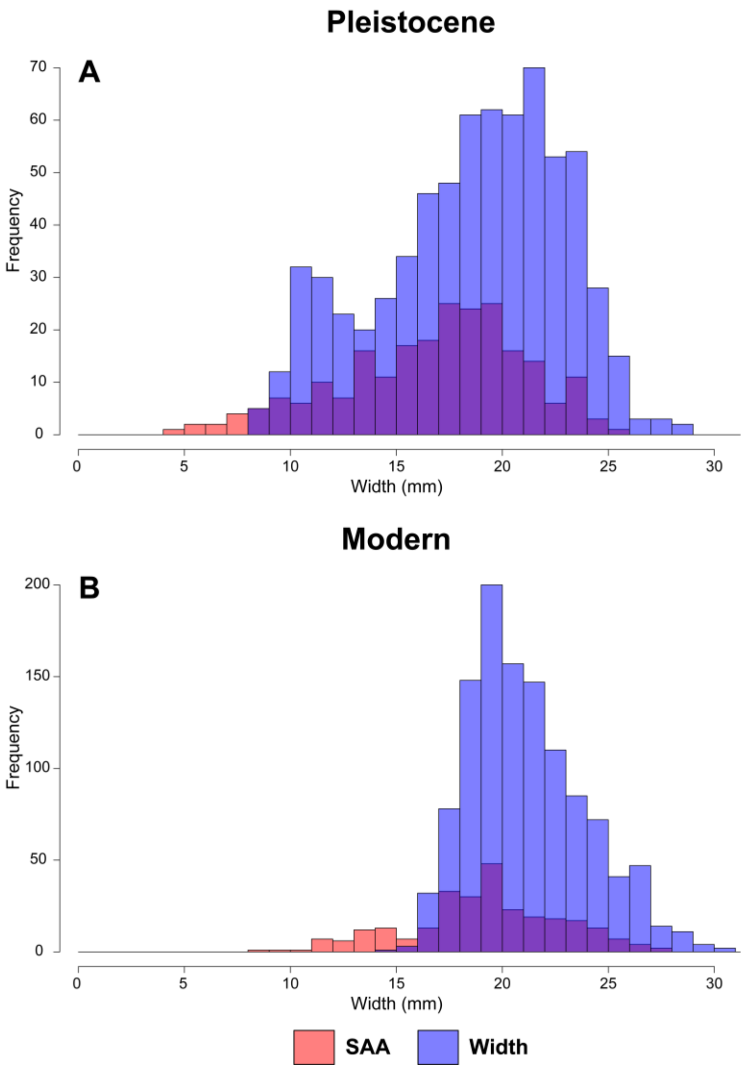

Figure 6.3

Histograms of SAA (red) and gastropod body size (blue). A. Pleistocene gastropods. **B.** Modern gastropods. The relative distributions of SAA and body size between Pleistocene and modern samples can be compared based on Fig. 5.3. Comparison of the SAA vs. body size distributions indicate how crab strength, relative crab success, and repair frequency might differ between the two samples. Both gastropod size and SAA are greater in the modern, indicating crabs are stronger. However, relative distributions of SAA vs. body size are similar between both, suggesting that any differences in repair frequency represent changes in the number of crab attacks, rather than a difference in crab relative success. If anything, relative success is greater in the Pleistocene (fewer repairs on smaller gastropods), indicating there are fewer repairs than expected in the Pleistocene compared to the modern.

Chapter 7

Conclusions

Human-induced climate change has become the most pressing issue for today's scientists. By combining modern experiments and surveys with fossil data, it is possible to understand how humans may, and possible already have, affect predator-prey relationships between crabs and their gastropod prey. The use of repair scars, while an incomplete dataset, can also be used to identify patterns of predation through both space and time. The results of this project indicate that the integrity of prey defenses will become increasingly vulnerable to predation under future ocean acidification. Furthermore, the rock crab fishery along the west coast of Canada and the U.S. is economically important, but is hampered by a lack of detailed data. I demonstrate that palaeontological practices, such as using repair scars on prey to understand crab predation, can be used to assess crab population abundance, and possibly crab size/health. Patterns of repair scars can then be compared across broad temporal scales, which may be particularly useful if historical records are incomplete or may have already been influenced by human activity. Hard-shelled prey, such as gastropods, provide a unique opportunity in which to investigate predation in the past, present, and possible future. Specifically, there were several important outcomes of this project:

1) Ocean acidification will decrease shell strength in calcifying organisms through dissolution of their shells, even if their growth is unaffected. However, not all shell structures will be impacted to the same extent, leading to potential shifts in predator-prey interactions and prey populations.

2) Reduced shell growth, whether due to changes in pH, or from predator cues, will only exacerbate the vulnerability of shells under future ocean acidification, as smaller shells are inherently weaker.
3) Shell microstructure, as much as composition, influences the amount of dissolution shells may experience, with fibrous calcite shell layers being more vulnerable than homogenous calcite layers.
4) The gastropod *Tegula funebralis,* shows more severe decreases in shell growth and strength, as well as more extensive dissolution, than *N. ostrina*, which shows no change in growth and experiences less shell dissolution/reductions in shell strength when exposed to decreased seawater pH.
5) The red rock crab, *Cancer productus,* is most likely to attack the first gastropod it recognizes, and then attack an adjacent gastropod, regardless of species.
6) Of three similar, co-occurring species of the gastropod *Nucella*, crabs show a preference for the largest, *N. lamellosa*, but this is most likely due to their inability to recognize the smaller two gastropod species as potential prey consistently.
7) Repair scars in the gastropod *T. funebralis* along the west coast of Canada and the U.S. indicate strong regional, rather than latitudinal, patterns of predation.
8) By measuring the size at which repair scars occur, it is possible to evaluate repair scar frequency and success independently. Even if the size of repairs change, if they remain relative to the distribution of the overall gastropod population size, repair frequency will not be affected. Repair frequency is therefore a fairly robust measure of the number of attacks observed.

9) Crabs in Oregon appear more successful/less likely to fail than in other regions, which has potentially selected for larger gastropods in the area.
10) Repair frequency (crab attack frequency) along the modern coast of Canada and the U.S. is greatest in B.C. and northern California, and lowest in southern California.
11) *T. funebralis* size, as well as the size of repairs, has increased since the Late Pleistocene, suggesting a potential "arms race" between gastropods and crabs, although it is possible that crabs are not as successful today as they were in the Late Pleistocene.
12) There are fewer repairs (crab attacks) in southern California today than there were in the Late Pleistocene, suggesting that crabs populations in southern California today may already be experiencing negative consequences from human activity.

Crabs and their gastropod prey provide an excellent model system in which to explore predator-prey interactions through time. Modern baseline studies to understand how prey defenses are impacted by changes to ocean chemistry and mechanisms of prey selection by crabs, combined with surveys of both modern and fossil repair scars, provides useful applications for the study of predation in the past, present and future. The fields of ecology and palaeontology have much to benefit from one another, and this project can provide a framework for continued interdisciplinary investigations that have applications for both fields.

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