

MEASUREMENT AND INTERPRETATION OF RATES OF SHELL REPAIR DUE
TO PREDATION

by

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Abstract

Repair scars, traces left by a failed attack on a prey item, provide direct evidence of predation in the fossil record modern systems without preservation or observation of predation events themselves. Counting repair scars and calculating repair frequencies, the number of scars in an assemblage relative to the number of individuals, allows a comparison of predation between assemblages in the fossil record and modern systems. However, because repair scars represent unsuccessful predation and not mortality, there are still questions concerning the measurement and interpretation of repair frequencies. Here, this thesis answers two of these questions relevant to taxa that are commonly used in repair scar studies: 1) can accurate repair frequencies can be measured samples of disarticulated bivalved prey and 2) how do predator size, prey size and prey species affect the likelihood of crab-gastropod encounters resulting in repair scars?

At present, repair scar studies only use articulated specimens but, because of this, repair scar studies are likely biased against taxa and environments that tend to be represented by disarticulated (single-valve) specimens. Using a temporally extensive dataset of articulated Paleozoic concavo-convex brachiopods this study investigates whether this exclusion is justified by measuring articulated and single-valve repair rates from the same specimens. I found that single-valve repair frequencies closely tracked true repair frequencies with an average of 93% of scars represented by the single valve (dorsal or ventral) with the greatest repair frequency. This high degree of accuracy was largely because the majority of scars (54%) occurred on both valves as the result of a single attack.

In modern temperate intertidal crab-gastropod systems, repair frequencies have been demonstrated to reflect predator density. However, while the interactions between crabs and

gastropods are well understood in a mechanical sense, it is not clear under what conditions these encounters lead to the generation of repair scars. Here, this study uses arena experiments to investigate how the predator size, prey size and prey species affect the likelihood of predator success (prey is killed) or failure (prey survives, and a repair scar could be generated). These experiments involved the crab, *Cancer productus*, and two of its common gastropod prey, *Nucella ostrina* and *Tegula funebris*. Regression models indicate that predator size has an effect on crab-gastropod encounters with encounters between larger predators being more likely to be successful. It was found that *C. productus* was more likely to fail in encounters with *T. funebris* than those with *N. ostrina*. In addition, encounters with *T. funebris* were much longer in duration than those with *N. ostrina*. Field data show that *T. funebris* populations tend to have greater repair frequencies than coexisting *N. ostrina* populations.

Considering the main objectives of this study: 1) single-valve repair frequencies were found to record the same trends in repair frequency as do articulated repair rates supporting that repair frequencies from disarticulated samples can be used in repair scars studies. 2) it was found that larger predators are more likely to be successful in crab-gastropod encounters and that *T. funebris* was more likely to survive encounters than *N. ostrina*. Considering this, the lower repair frequencies measured in *N. ostrina* populations relative to *T. funebris* encounters are likely due to the much higher rates of predator success in *N. ostrina* encounters.

Preface

Chapter 1 of this thesis has been submitted for review as: Mendonca, Steven E., Pruden, Matthew J., Dievert, Rylan R., and Leighton, Lindsey R. Is one valve enough? The utility of single valve repair frequencies in predation studies. I was responsible for all data collection, analysis, and composition of the manuscript, tables, and figures. Pruden, Matthew J., and Dievert Rylan R., assisted with data collection. Leighton, Lindsey R. was the supervisory advisor and assisted in editing the manuscript. The chapter has been submitted to *Paleobiology*.

Chapter 2 of this thesis has previously been reviewed as: Mendonca, Steven E., Barclay, Kristina M., Tyler, Carrie L., and Leighton, Lindsey R. Intrinsic factors affecting predator success in crab-gastropod encounters and their implications for repair frequencies. I was responsible for data collection in arena experiments and all analysis, and composition of the manuscript, tables, and figures. All authors assisted with data collection in the arena experiments and editing the manuscript. Tyler, Carrie L., and Leighton, Lindsey R. supplied previously collected repair scar data for *N. ostrina* and *T. funebris*. Leighton, Lindsey R. was the supervisory advisor. The chapter has been resubmitted to the *Journal of Marine Biology and Ecology* as a new submission.

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Introduction

Studying predation is difficult because interactions between predators and prey are very rarely preserved in the fossil record and are difficult to observe in modern systems. However, unsuccessful predation that results in observable deformities (repair scars) on the mineralized components of prey, such as shells, provides an opportunity to study direct evidence of predation without observation of predation event itself (Schindel et al., 1982; Schoener, 1979; Stafford et al., 2015b; Vermeij, 1982a). In the case of taxa which grow by accretion such as bivalves and brachiopods, these repair scars permanently record an encounter between predators and prey and can be used to study predation in both modern and fossil systems (Alexander, 1981; Alexander and Dietl, 2003; Kowalewski, 2002; Leighton et al., 2013; Schindel et al., 1982; Stafford et al., 2015a; Vermeij, 1982b, 1982a). Repair scars are typically used by calculating a repair frequency: the number of repair scars in an assemblage or prey population relative to total assemblage or population size. These repair frequencies can then be used to study how predation varies across assemblages and prey populations through time and space. For example, repair frequencies from fossil assemblages have been used to evaluate how predation pressure has influenced the evolution of predators and prey (Alexander, 1981; Johnsen et al., 2013; Kowalewski et al., 2005; Leighton et al., 2013; Vermeij, 1987). Similarly, in the modern, repair frequencies in temperate crab-gastropod have been found to proxy predator abundance (Molinaro et al., 2014b; Stafford et al., 2015b; Tyler et al., 2019) thus serving as a useful tool for determining how predation affects the distribution and ecology of prey. However, because repair frequencies reflect unsuccessful predation and not mortality, there are still many questions about how to measure and interpret repair scars. The objective of this study is to further the current understanding of repair frequencies by 1) determining if accurate repair frequencies can be measured from samples of

disarticulated bivalved prey and 2) determining how predator size, prey size and prey species affect the likelihood of crab-gastropod encounters resulting in repair scars?.

Repair frequencies are difficult to interpret because they are dependent on attack frequency, the number of encounters that a prey population is subjected, and success rate, the likelihood of each attack resulting in predator success (Alexander, 1986a; Kowalewski, 2002; Leighton, 2003; Vermeij, 1982a). The more often a predator-prey encounters occur, the more chances there are for a repair scar to be generated. The more likely a predator is to be successful, the more likely the prey is to be killed in which case no scar can be preserved. This leads to problems interpreting repair frequencies because if there are a high frequency of attacks, there are likely to be a high number of repair scars but, if the predator making these attacks is highly successful in killing its prey, it may leave few repair scars. It is unclear if variation in repair frequency reflect changes in attack frequency or predator success frequency or some combination of both.

Bivalved prey, such as brachiopods and bivalves, are ideal study subjects for repair scar studies because they have high preservation potential, grow by accretion, and tend to be abundant in many different fossil and modern environments. However, they are prone to disarticulation. This is a problem because repair frequencies between different valves may vary if one valve is more likely to fail when attacked (variation in success rate) or if a predator preferentially attacks one valve over the other (variation in attack frequency). If repair frequencies varied significantly between valves, it would not possible to derive the per individual repair frequency that would normally be used to interpret differences in predation between different prey populations. At present, repair scars studies avoid disarticulated material but, this comes with the risk of underrepresenting the taxa and depositional environments commonly

represented by disarticulated samples. However, the assumption that disarticulated samples produce inaccurate repair frequencies has never been tested and some researchers have observed that matched scars (scars occurring on both valves at the same location resulting from a single attack) are common (Alexander, 1990, 1989). If these matched valves are common enough, repair frequencies on either valve would be very similar. To test whether disarticulated samples convey accurate repair frequencies, this study will use articulated brachiopod samples to measure both articulated and disarticulated repair frequencies. If disarticulated repair frequencies show the same patterns in repair frequency as articulated samples, this would allow inclusion of disarticulated samples in repair scar studies.

In modern systems, recent study has demonstrated that repair frequencies reflect predator abundance in temperate crab-gastropod systems (Molinaro et al., 2014a; Stafford et al., 2015b; Tyler et al., 2019). Furthermore, these repair frequencies have been found to be buffered against short term disturbances and therefore record the baseline predation frequencies that would normally require long term observation (Tyler et al., 2019). However, there is still the question of how the generation of repair scars in individual encounters result in these trends in population level repair frequencies: It is not clear how factors such as predator and prey size affect the outcomes individual encounters. Resolving this problem would be to be able to predict the outcomes of crab-gastropod encounters based on the conditions of the encounter relate these predictions to population level repair frequencies. This study will contribute to solving this problem by observing crab-gastropod encounters and determining how predator size, prey size, and prey species affect the outcome and duration of these encounters. A model will be derived from these observations and compared with repair frequencies measured from natural

populations to determine how the conditions affecting the outcome of individual encounters relate to repair frequencies.

The first chapter of this thesis will analyze how repair frequencies vary between articulated and disarticulated brachiopod samples in the fossil record to determine if repair frequencies from single-valve samples can be used in repair scar studies. The second chapter will observe crab-gastropod encounters between different sized predators, *Cancer productus*, and prey, *Tegula funebris* and *Nucella ostrina*, in order to determine how predator size, prey size, and prey species affect the probability of a crab-gastropod encounter resulting in a repair scar. Here, this combined approach using fossil data and modern experiments will provide insight into the measurement and interpretation of repair scars and thereby facilitate studies on the effects of predation on the evolution and ecology of organisms.

1 Chapter 1

Is one valve enough? The utility of single valve repair frequencies in predation studies

1.1 Introduction

Encounters between shelled prey and durophagous (shell-crushing) predators can be preserved permanently as a repair scar when the shelled prey survives an encounter and repairs its shell (Alexander, 1986a, 1981; Schoener, 1979; Vermeij, 1982a). These traces are crucial to understanding predation in the fossil record as they record direct and quantifiable evidence of encounters between predators and prey. Analysing predation using traces is complicated by disarticulation of prey specimens or preservation such that only a single valve may be observable. Counting traces using single valves alone could lead to missing information if there are uncounted traces on the missing valve. Alternatively, if a single attack produces traces on both valves of an individual that was mistakenly counted as two individuals, this would double counting of traces and inflate repair rates. As many taxa (e.g., heteroconch bivalves, brachiopods with deltidodont dentition) frequently disarticulate after death and even articulated specimens may sometimes only reveal a single valve (e.g., the opposite valve is embedded in rock), solving this “single valve” problem could increase available data. Despite hesitation by paleontologists to use repair frequencies based on single valves due to the chance that they are not likely to reflect “true” repair frequencies, the severity of this problem has never been tested. The goal of this study is to address this issue by calculating single-valve repair frequencies on brachiopods, a bivalved taxon which has been used often to assess crushing predation in the Paleozoic, to determine if and/or how single-valve repair frequencies vary with respect to true repair frequencies.

During the Paleozoic, brachiopods dominated (in the sense of diversity and abundance) the communities of many environments and, because of their mineralogy, they typically preserve well enough for reliable identification of repair scars (Alexander, 1986a). Repair scars are quantitative, direct-evidence records of predator-prey encounters and consequently, repair scars on brachiopods have been used extensively to study durophagous predation in the fossil record (Alexander, 1989, 1986b, 1986a; Harper, 2005; Huntley and Kowalewski, 2007; Johnsen et al., 2013; Leighton, 2002, 1999; Leighton et al., 2013; Richards and Leighton, 2012; Tyler et al., 2013; Vermeij et al., 2006). Predation in the Paleozoic has been of particular interest because of the major radiations of durophagous predators, specifically jawed fish and concurrent evolution of anti-predatory adaptations in prey during the mid-Paleozoic which suggest that predator-prey interactions had a significant effect on the evolution of Paleozoic fauna (Baumiller and Gahn, 2004; Brett and Walker, 2002; Sallan et al., 2011; Signor and Brett, 1984). In combination with the known framework of evolutionary trends in Paleozoic predators and prey, repair scars provide an opportunity to test inferences about the mechanisms by which anti-predator defenses evolved in brachiopods during the Paleozoic.

Concavo-convex brachiopods (Class Strophomenata) have been of particular interest in studying Paleozoic predator-prey interactions as they tend to have repair frequencies an order of magnitude greater than biconvex taxa (Alexander, 1986b; Leighton et al., 2013; Pruden et al., 2018). It is unclear whether these differences in repair frequency reflect differences in predation frequency and/or differences in the group's ability to withstand predation. Microstructure, shape, and adaptations such as plicae may have made biconvex shells relatively stronger overall but also more likely to experience catastrophic failure instead of repairable damage (Alexander, 1989). In any case, concavo-convex brachiopods represent the vast majority of available repair scar data

for the Paleozoic (Alexander, 1986a, 1986b). This is problematic because this particular clade is commonly preserved as single valves. This preservation issue is due to a combination of their deltidont dentition, which is more prone to disarticulation than many other brachiopod groups (Carlson, 1989) and differential preservation potential of valves; concave valves (the flatter, less convex valve) are better preserved in disarticulated specimens as they tend to be thicker and more resistant to taphonomic processes (Alexander, 1989). Additionally, the convex valve can become preferentially preserved when the concave valve of an articulated specimen is infilled with sediment leaving only the convex valve observable.

Some depositional settings promote disarticulation or modes of preservation that only allow observation of a single valve and therefore would be excluded from repair scar studies. For example, on well cemented limestone or sandstone slabs, only a single valve may be observable. Many taphonomic situations that promote single-valve preservation such as infilling of one valve or slab-type preservation could potentially be avoided with extensive sample preparation of samples or smaller sample sizes but, this is rarely feasible in the case of repair scars studies. Repair scar studies require representative sample sizes and need to avoid potential biases that would be introduced by non-random sampling. At present, exclusion of samples dominated by single-valve preservation results in the very real possibility that certain taxa and environments, such as those that are preserved as slabs, might be systematically excluded from repair scar studies: brachiopod repair scar studies at present are heavily biased towards shales (e.g., Alexander 1986*b*; Richards and Leighton 2012; Johnsen et al. 2013; Leighton et al. 2013). Overrepresentation of shales in repair scar studies may be introducing significant bias in studying predation in the past, especially in studies of repair scars through time, in which case more extensive coverage of environments and taxa would be beneficial.

The primary reason that single-valve samples are not currently used in repair scar studies is because there is a chance that repair frequencies may be different between valves of the same sample. This could occur due to differences in the strength of the valves or predator stereotypy. The tendency for repair scars to occur at different relative frequencies between valves is referred to here as valve affinity; e.g., a specimen with dorsal valve affinity has higher repair frequencies on the dorsal valve than on the ventral valve.

In the context of predator-prey interactions, the probability of repair scars occurring is dependent on two different factors which could vary between dorsal and ventral valves. The first factor, success rate, is the likelihood that a given predator-prey encounter will result in predator success. If the predator is successful, the predator kills its prey and the prey item is crushed and not preserved. Alternatively, if the predator fails to kill its prey and the prey survives, a repair scar will be formed. The probability of success with respect to each valve is dependent on the valve's mineralogy and thickness but also on the valve's geometry which can dictate whether fractures are more likely to be localized and repairable or propagate and result in catastrophic failure (Alexander, 1989). Considering single valve repair frequencies, if two valves are attacked independently at the same frequency by the same predator, the stronger valve will have a greater frequency of repair scars because the predator will have a lower rate of success and be more likely to produce repairable damage. Attacks on the weaker valve would be less likely to be preserved due to the predator being more likely to kill (and destroy) its prey.

The second factor which affects the probability of repair scars occurring is the attack frequency. If the valves are the same strength, if one valve is attacked more often, that valve will tend to have higher repair frequencies. This could be due to predator preference for one valve or ease of access due to the brachiopod's orientation. For concavo-convex brachiopods this second

point is particularly relevant as they sit on one of the valves, obscuring this valve from predators. With the combined effects of varying attack frequency and predator success rate, the fear of valve affinity and related bias occurring is not unwarranted.

While valve affinity conceivably can occur, it is not definite that it does occur. Single-valve predation would be affected by the factors listed previously, but there are also attacks that occur simultaneously on both valves (referred to here as matched-valve attacks). Matched-valve attacks reflect instances in which a jawed or chelate attacker grappled the prey from both sides of the commissure simultaneously, such as a durophagous fish taking a closed brachiopod between its jaws. This results in matched repair scars on both valves of the brachiopod. Though it has not been quantitatively tested, matched-valve attacks are common enough that the occurrence of matched damage on both valves is used to aid in identification of repair scars (Alexander, 1986a). The prevalence of matched-valve attacks is not surprising given that the reaction of a bivalved organism to a perceived predator is to close its valves inhibiting access to soft tissue. Furthermore, even single valve attacks such as those involving prying open a closed brachiopod could result in damage to both valves. If the great majority of repairs are the product of these matched scars, there would be little valve affinity and single-valve repair frequencies would vary little from the repair frequencies of articulated specimens.

Valve affinity may be dependent on the morphology of predators and prey and therefore may change over time in concert with changes in predator-prey interactions induced by the evolution of new taxa and adaptations. Many of the features that differ between valves, such as shell ornament, spines, and thickness, have been interpreted to be adaptations to predation (Alexander, 2001; Dietl and Kelley, 2001; Johnsen et al., 2013; Leighton, 2001, 1999; Leighton, 2003; Signor and Brett, 1984). During the mid-Paleozoic, there is a major radiation of

specialized jawed predators and concurrent anti-predator defenses in prey (Brett, 2003; Brett and Walker, 2002; Signor and Brett, 1984). This faunal change could have had drastic effects on predator-prey interaction as predators with different tools for taking prey are also likely to employ different behaviours. Similar to modern crabs, which chip away at the apertures of gastropod prey or pry open valves of bivalved prey if they are unable to crush them outright (Bertness and Cunningham, 1981; Juanes and Hartwick, 1990; Zipser and Vermeij, 1978), shell crushing predators that are not strong enough to damage both valves of their prey may be limited to prying and chipping away at a single valve. Early invertebrate predators might have been limited to attacks on single valves, as many of them are thought to have lacked adequate jaw or chelate structures to break shells consistently (see Signor and Brett 1984). This could be the case for pre-Devonian arthropod and cephalopod characters which lacked the mineralized apparatuses common in more recent durophagous invertebrates (Gasiowski, 1973; Schram, 1979; Vermeij, 1983). Jawed vertebrate predators which radiated in the Devonian (Sallan et al., 2018) may have been stronger and therefore more likely to make matched-valve attacks than previous durophages such as arthropods and cephalopods. In contrast to pre-Devonian invertebrate predators, early durophagous vertebrate predators, such as placoderms and boney fish, bear clear shell crushing adaptations similar to those found in modern durophagous taxa (Moy-Thomas and Miles, 1971; Romer, 1966). Furthermore, jawed vertebrate predators may have handled their prey differently than arthropods and cephalopods which could also lead to a change in whether single or both valves are damaged. Without a concrete understanding of pre-Devonian durophages, it is difficult to determine whether durophagous vertebrates were necessarily stronger or handled their prey differently relative to their invertebrate predecessors, but this possibility presents a potential source of temporal biases in single valve repair rates that must be tested.

This study determines how single valve repair frequencies vary relative to articulated repair frequencies in brachiopods using a temporally extensive Paleozoic dataset. The dataset includes a diversity of species representing some of the most abundant concavo-convex brachiopods of the time, which make up the bulk of the available repair scar data for Paleozoic brachiopods (Alexander, 1986b). In order to determine if single-valve repair frequencies would differ from the repair frequencies of articulated specimens, both articulated and single-valve (ventral or dorsal) repair frequencies are collected from articulated specimens and compared. If single-valve repair frequencies are accurate representations of true repair frequencies, dorsal and ventral single-valve repair frequencies will vary little from true repair frequencies and any trends in true repair frequencies will be evident in single-valve repair frequencies.

1.2 Methods

1.2.1 Data collection

Concavo-convex brachiopods (Class Strophomenata) from the National Museum of Natural History (NMNH) collections and the personal collections of author Leighton ranging from the Ordovician to Permian in age were sampled (Table 1.1). Each sample is a collection of specimens from a specific species-location-time combination. Leighton samples were collected by that author over the last decade; while these samples were not collected specifically for this study, all samples were collected for the purpose of examining predation. NMNH samples were subsequently chosen to fill gaps in time and taxa. While similar in overall morphology, the selected taxa host a variety of features that could be defenses against predators such as spines, geniculations, and rugae. The samples consist of taxa common to a broad region of North America, but generally constituted a single biogeographic province during any given time period. Only articulated brachiopods with greater than 50% of both valves visible and the preservation

adequate to identify repair scars (i.e., visible growth lines) were used. Samples from similar paleoenvironmental conditions were used to reduce the effects of environment, although it should be noted that general patterns in valve affinity across space and time would indicate a robust signal. In total, the samples included 1034 individual brachiopods with an average sample size of 68.93.

Using a dissecting microscope, crushing repair scars were identified and categorized according to the valve on which they occurred. Unrepaired damage was not counted. Repair scars were recorded as either matched on both valves, on the dorsal valve only, or on the ventral valve only. Matched scars are those that result from a matched-valve attack, in which case both valves were damaged simultaneously in the same attack; e.g., a predator biting a closed brachiopod on both sides. Following previously established methods (Alexander, 1989; Richards and Leighton, 2012), matched and single valve scars were differentiated by measuring the distance from the outermost affected growth line to the hinge line for each scar. If the measurements are the same, they are from the same attack and indicate that both scars occurred at the same time in ontogeny.

1.2.2 Data analysis

To determine if repair frequencies from single valves are comparable to articulated repair frequencies, articulated specimens were used to generate both the articulated repair frequencies (the “true” repair frequencies) and the dorsal and ventral valve repair frequencies separately. This was done to simulate the repair frequencies that would be derived from disarticulated single-valve assemblages (referred to as single-valve repair frequencies). When the following methods refer to single-valve or articulated specimens, these are the same specimens but “single-valves” refer to either all dorsal or all ventral valves of the sample, while “articulated” valves or

specimens refers to whole brachiopods. The number of scars on articulated valves/specimens will not necessarily be the sum of the number of scars on the dorsal and ventral valves because of matched scars, which would occur as separate scars on both single valves but only count as one scar on the articulated specimen.

There are two different metrics to measure the relative number of repair scars in an assemblage, both of which are calculated in most repair scar studies (Kowalewski, 2002; Leighton, 2002). In this study, “repair frequency” is an umbrella term referring to either metric. The first metric, “repair rate”, abbreviated as Rr (=RF1 of Pruden et al. 2018, Molinaro et al. 2014), is the total number of repair scars in an assemblage divided by the total number of individuals in that assemblage. This is the ratio of repair scars to individuals in an assemblage presented as a decimal and it can have a value > 1 , as individual brachiopods can have more than one scar.

The second metric, “proportion repaired” abbreviated as %R (=RF2 of Pruden et al. 2018, Molinaro et al. 2014), is the number of individuals in an assemblage with at least one scar divided by the total number of individuals in that assemblage. This number ranges from 0% to a maximum value of 100%. %R is the proportion of individuals in a prey assemblage that have at least one scar.

Articulated and single-valve repair frequencies were calculated using both metrics; %R and Rr. This was done for consistency with the literature, but also to determine if the choice of metrics had any effect on the deviation of single valves repair frequencies versus that of the articulated specimen.

The accuracy of single-valve repair frequencies is measured by determining the proportion of scars or scarred individuals of articulated specimens represented by a single valve. In the case of R_r, this would be the number of scars represented by a single valve divided by the number of scars on articulated specimens. In the case of %R, this would be the number of single valves with at least one scar divided by the number of articulated specimens with at least one scar. Using either metric, the percentage resulting is the proportion of scars or scarred individuals represented by a single valve where 100% indicates agreement between articulated and single valve repair frequencies. The valve and metric that consistently produces results closer to 100% would be a more accurate measure of single-valve repair frequencies.

Regardless of the accuracy of single-valve repair frequencies, these frequencies would still be useful if they preserved the relative patterns and trends observed in articulated repair frequencies. To test whether the relative rank order of samples was preserved by single-valve repair frequencies, a Spearman's rank correlation was used. If trends in articulated repair frequencies are preserved in single-valve repair frequencies, I would expect a significant result with a high correlation coefficient.

Valve affinity (VA) is the tendency for scars to occur more often on one valve than the other and was calculated using the formula:

$$VA = \frac{SC_d - SC_v}{SC_d + SC_v}$$

where sc_d is the number of scars on the dorsal valves and sc_v is the number of scars on the ventral valves. Positive valve affinity indicates dorsal valve affinity and negative valve affinity indicates ventral valve affinity. Valve affinity has a maximum value of one, in which case all scars only occur on the dorsal valve only, and a minimum value of negative one, in which case

all scars occur on the ventral valve only. A value of zero indicated that there are an equal number of scars of both valves.

The evolution of new predators over the course of the Paleozoic may have led to changes in valve affinity or the ratio of single to matched valve scars through time due to changes in predator strength and behavior. To determine if valve affinity or the proportion of matched scars changes directionally through time, a Spearman's rank correlation between these variables and the relative stratigraphic order of samples was used. This correlation was evaluated using Kendall's Tau-b, a parameter that allows for an accurate calculation of the correlation coefficients and p-value when ties occur.

1.3 Results

Measurements of single-valve repair rate and proportion repaired closely tracked articulated repair frequencies when using the greater of the two single-valve repair frequencies for each sample (ventral or dorsal). The rank order of articulated repair frequencies between samples was preserved in both %R and Rr measurements (Tables 1.2, 1.3, Figs 1.1, 1.2, 1.3). Single-valve Rr had an average accuracy of 82.1% for ventral valves and 73.8% for dorsal valves (Fig 1.4). Single-valve %R showed similar results with an average accuracy of 85.7% for ventral valves and 73.6% for dorsal valves (Fig 1.4). Using either the dorsal or ventral single valves provided much more accurate results than adding the scars on both valves together, which produced much greater repair frequencies than articulated repair frequencies (mean of 154% for Rr and 159% for %R). Choosing the valve with the greatest %R or Rr for each sample, in accordance with Leighton (2011), provided the most accurate single-valve measurements with an average accuracy of 93.1% for Rr and 93.3% for %R.

Matched-valve scars were more common than single-valve scars, making up the majority of scars in 12 of 15 samples with an average of 54% of total scars per sample (Table 1.2, Fig 1.3). Of the single-valve scars, ventral-valve scars were the most common in 8 of 12 samples. There was no correlation between stratigraphic order of samples and valve affinity ($\tau = 0.29$, $p = 0.13$) or the proportion of matched scars ($\tau = 0.22$, $p = 0.27$).

1.4 Discussion

1.4.1 *Using single valves to measure repair frequency*

Valve specific repair frequencies closely tracked articulated repair frequencies regardless of whether the ventral or dorsal valves were used (Figs 1.1, 1.2). When using the single valve with the greater repair frequency for each sample, the average accuracy of single-valve R_r measurements and %R measurements was 93.1% and 93.3% respectively. Additionally, using either ventral or dorsal valve alone preserved the relative rank order of samples (Figs 1.1, 1.2). This close tracking of single-valve and articulated repair is largely because matched-valve scars (scars that occur on both valves and result from a single attack) were the most common scars in most samples (Fig 1.3). These results corroborate that single-valve repair frequencies are comparable to articulated repair frequencies in strophomenate brachiopods.

Dorsal and ventral valves showed the same trends in repair frequency as did articulated repair frequencies though one of the two valves were usually more accurate. The more accurate valve was always the one with the greatest number of repair scars, as single valves can only give repair frequencies less than or equal to the articulated repair frequencies. Our results were consistent with the methodology proposed by Leighton (2011): using the valve that presents a higher repair frequency in disarticulated samples gives repair frequencies very close to the true articulated repair frequency and justifies using the single valve with the greatest repair frequency

in the case of disarticulated specimens. Using the valve with the greatest repair frequency gave the best overall accuracy, however, in most cases, the more accurate valve was the more convex ventral valve and the single-valve frequencies of either valve still gave accurate results.

Considering this, the best practice for using single-valve repair frequencies would be to use the valve with the greatest repair frequency when available, but single-valve repair frequencies from either valve can also be used especially in the case of the convex valve.

1.4.2 Valve affinity through time

There is no apparent trend in the valve affinity or the proportion of matched scars through time, despite the radiation of jawed durophagous predators during the Devonian. The Devonian radiation of durophagous fish, which likely preyed upon brachiopods (see Alexander 1981), did not significantly change how predators interacted with prey in the context of valve affinity. It might be expected that matched valve attacks would increase through time as Devonian and later predators including jawed fish may have been stronger and more capable of attacking both valves simultaneously than pre-Devonian predators. Alternatively, the opposite could be expected if matched valve attacks made by vertebrates and post-Silurian predators were more likely to succeed and thus leave fewer scars. However, despite uncertainty in the ability of proposed pre-Devonian durophagous predators and differences, these early predators were responsible for a similar proportion of matched-valve and single-valve attacks as later, more specialized Paleozoic durophages. Consequently, single-valve repair frequencies are not biased by age in Paleozoic brachiopod assemblages.

1.4.3 Ventral valve affinity

In the instance of single-valve predation, the valve that is attacked more often and is more likely to withstand predation should have greater repair frequencies (see Vermeij 1982;

Alexander 1989). Both productides and strophomenides have ventral valve affinity which indicates that, if single-valve predation was occurring, the ventral valve should be attacked more often and/or be more resistant to attacks by predators. For concavo-convex brachiopods, frequency of attack could vary due to life orientation. Productides are thought to have lived with their convex ventral valve facing down, resting on the sediment and slightly buried (Grant, 1966). This orientation would obscure the ventral valve leaving the dorsal concave valve more exposed when the brachiopod's valves are gaping. Therefore, the finding that productide samples show ventral valve affinity is opposed to what would be expected if the prey's orientation had a significant effect on valve affinity as the ventral valve would be obscured. This might indicate that it is very rare for single-valve attacks to occur or be preserved when the brachiopod is gaping. While the brachial valve is more accessible when the brachiopod is gaping in a convex ventral-valve down orientation, the brachial valve may actually be harder to attack when the brachiopod is closed as it is recessed in the larger convex ventral valve. Single-valve predation on gaping prey may also be unlikely to result in a repair scar because, when it occurs, the predator would already have access to the brachiopod's soft tissues negating the brachiopods primary defenses and likely result in death of the prey rather than survival and generation of a repair scar.

The convex down orientation may also have been the case for strophomenide brachiopods, but this is controversial. Except for *Strophomena*, the convex valve is the ventral valve and the concave valve is the dorsal valve for all taxa in this study. There are arguments for both convex-down (Alexander, 1975; Leighton, 2005, 1998) and convex-up (Dattilo, 2004; Plotnick et al., 2013) orientations. The ventral valve affinity observed in strophomenide samples here would be more consistent with the convex-up orientation but, the finding that productides

also exhibit ventral valve affinity and lived convex-down makes it inappropriate to infer life position for strophomenide brachiopods from repair scars.

Differences in predator success could explain valve affinity if it varied between brachiopod valves due to valve strength. If single-valve predation was occurring and the valves were attacked at similar rates, the stronger of the two valves should have higher repair frequencies because the organism would be more likely to survive damage to that valve than the other. In strophomenide brachiopods, the stronger valves would typically be the dorsal valve which is generally thicker than the ventral valve and has brachial ridges which would have made damage less likely to be lethal by reducing the chances of fractures propagating deeper into the mantle cavity (Alexander, 1990, 1989). This could also be the case for productides, which also have brachial ridges on their dorsal valves, but it is not clear if the ventral valve is thinner than the dorsal valve as it is in most strophomenides. Here, this study found ventral valve affinity in both strophomenides and productides, contrary to our prediction that the stronger brachial valve should have more repair scars. A possible explanation in the context of valve strength is that true single-valve predation is uncommon, and that most single-valve scars result from the ventral valve being damaged first in matched-valve attacks. In this case, repair scars could preferentially occur on the weaker valve. For example, when modern crabs attempt to crush bivalved prey, such as oysters or mussels, it is not uncommon for one valve to fail while the other remains intact (personal observation, Leighton). This conclusion is also consistent with the prevalence of matched-valve scars in all samples.

1.4.4 Valve affinity and morphology

Most samples had ventral valve affinity but the few that had dorsal valve affinity were similar in morphology. This may indicate a relationship between valve affinity and brachiopod

morphology. The two genera with the greatest dorsal valve affinity were *Rafinesquina alternata* and *Homoleptostrophia uniformia*. Both taxa are large, relatively flat/planar brachiopods (*R. alternata* was not strongly geniculate in our specific samples). While matched scars still make up a great proportion of the total number of scars on these taxa, single-valve scars on the ventral valve are nearly absent. Dorsal valve affinity would be predicted knowing the greater strength of the dorsal valve in these samples (Alexander, 1990, 1989). This is in contrast to ventral valve affinity which, as discussed previously, is contrary to what would be predicted by differences in valve strength. The dorsal valve affinity and high repair frequencies measured in *R. alternata* and *H. uniformia* indicate that these brachiopods could have experienced very different interactions with their predators, possibly experiencing much more targeted single-valve predation than other taxa.

Oepikina lirata also had dorsal valve affinity. While ventral valve affinity and repair frequency of the *O. lirata* sample is less than those of *R. alternata* and *H. uniformia*, this example is particularly interesting because it is less convex than the similar species of the same genus *O.inguassa*, which has ventral valve affinity. This is another example which may support an association of dorsal valve affinity with more planar, less convex brachiopod morphologies. However, this example also casts doubt on a universal explanation of valve affinity via convexity as *O. lirata* is very similar in convexity to other species such as *Strophodonta* which has ventral valve affinity. The qualitative relationship between valve affinity and morphology discussed here requires more investigation to determine whether this association of convexity with dorsal valve affinity is unique to specific taxa or samples.

While dorsal valve affinity occurs in the previously discussed strophomenide taxa, there are no examples of dorsal valve affinity in productide taxa, suggesting that there could be a

difference in valve-affinity between taxonomic groups. This could be due to convexity as there are no productide brachiopods that are morphologically similar to *R. alternate* and *H. uniformia* in this study. Though productide brachiopods originate in the Devonian while strophomenide brachiopods are virtually extinct by the end-Devonian, evolutionary changes in predators are not likely to explain the absence of dorsal valve affinity, given the lack of correlation between valve affinity and time. A correlation would be expected if predators, specifically durophagous fish which are present in the Early Devonian onwards (Brett and Walker, 2002; Moy-Thomas and Miles, 1971; Signor and Brett, 1984), were not making dorsal valve attacks as often as the durophagous predators preceding them. The absence of dorsal valve affinity in productide taxa is therefore likely due to their greater convexity or other features not shared with strophomenides, such as spines.

1.4.5 Conclusion

While valve specific repair frequencies did vary from articulated frequencies, the rank order of samples did not change significantly. The most accurate way to measure the repair frequencies of disarticulated assemblages is to use the single valve with the greatest repair frequency. The consistency between single-valve and articulated repair frequencies is largely due to the large proportion of scars that are matched scars resulting from a single attack. It is also likely that many single-valve scars may result from matched-valve attacks, especially in the case of ventral valve scars. Ventral valve scars possibly result from matched-valve attacks in which the weaker ventral valve fails, though this hypothesis requires confirmation that productide ventral valves tend to be weaker than their dorsal valves, as is the case in strophomenide taxa.

While there were no temporal trends in valve affinity, there may be an association between valve affinity and prey morphology. All but three taxa had an affinity for the convex

valve (the ventral valve in all taxa except *Strophomena*) and those with more scars on the concave dorsal valve were similar in morphology. However, even when including samples with dorsal valve affinity, single-valve repair frequencies measured from either valve still served as accurate proxies of true repair frequencies.

Table 1.1. Summary of samples and repair scars counted.

Sample Name	Taxon	Unit	Age	Sample Size	Number of Scars		
					Shared	Dorsal	Ventral
<i>Rtl.sp</i> Flor	<i>Reticulatia sp.</i>	Florena Shale	Permian	49	31	2	5
<i>Pj.neb</i> Flor	<i>Parajuresania nebraskensis</i>	Florena Shale	Permian	74	18	0	8
<i>Neo.sp</i> Pueb	<i>Neochonetes sp</i>	Pueblo	Permian	87	6	1	5
<i>Kt.las</i> Fin	<i>Kutorginella lasallensis</i>	Finis Shale	Pennsylvanian	58	7	2	4
<i>Pu.sym</i> Fin	<i>Pulcratia symmetrica</i>	Finis Shale	Pennsylvanian	77	26	4	19
<i>In.inf</i> Faye	<i>Inflatia inflata</i>	Fayetteville Shale	Mississippian	136	16	5	29
<i>Str.de</i> Sil	<i>Strophodonta demissa</i>	Silica Shale	Devonian	82	15	0	14
<i>Hl.uni</i> Sil	<i>Homoleptostrophia uniforma</i>	Silica Shale	Devonian	96	49	19	7
<i>Lt.acu</i> Har	<i>Leptaena acuticuspidata</i>	Haragan	Devonian	80	14	1	11
<i>Str.pl</i> Lib	<i>Strophomena planumbona</i>	Liberty	Ordovician	38	16	4	5
<i>Raf.al</i> Lib	<i>Rafinesquina alternata</i>	Liberty	Ordovician	50	38	33	0
<i>Lt.rcd</i> Wayn	<i>Leptaena richmondensis</i>	Waynesville	Ordovician	100	25	1	11
<i>Raf.al</i> Fair	<i>Rafinesquina alternata</i>	Fairview	Ordovician	61	16	32	2
<i>Oe.lir</i> Dec	<i>Oepikina lirata</i>	Decorah Shale	Ordovician	21	6	7	1
<i>Oe.ing</i> Dec	<i>Oepikina inguassa</i>	Decorah Shale	Ordovician	25	8	2	5

Table 1.2. Summary of sample repair frequencies, single valve accuracy and valve affinity. Valve specific repair frequencies were simulated using the single valves (dorsal or ventral) of these articulated specimens. Valve accuracy includes the proportion of scars (in the case of Rr, including matched-valve scars) or scared individuals (in the case of %R) represented by a single valve; 100% would indicate that all scars are represented by a single valve, and the single-valve repair frequency is equal to the true repair frequency. Valve affinity indicates which valve has more scars. Positive valve affinities indicate that more scars occur on the dorsal

valves than on the ventral valves, while negative affinity indicates that more scars occur on the ventral valves than on the dorsal valves.

Sample Name	Repair Rate (Rr)			Rr Accuracy		Proportion Repaired (%R)			%R Accuracy		Valve Affinity
	Rr	Rr _D	Rr _V	Dorsal	Ventral	%R	%R _D	%R _V	Dorsal	Ventral	
<i>Rtl.sp</i> Flor	0.78	0.67	0.73	86.8%	94.7%	59.2%	55.1%	57.1%	93.1%	96.6%	-0.08
<i>Pj.neb</i> Flor	0.35	0.24	0.35	69.2%	100.0%	33.8%	24.3%	33.8%	72.0%	100.0%	-0.31
<i>Neo.sp</i> Pueb	0.14	0.08	0.13	58.3%	91.7%	12.6%	8.0%	11.5%	63.6%	90.9%	-0.33
<i>Kt.las</i> Fin	0.22	0.16	0.19	69.2%	84.6%	19.0%	13.8%	15.5%	72.7%	81.8%	-0.15
<i>Pu.sym</i> Fin	0.64	0.39	0.58	61.2%	91.8%	50.6%	29.9%	48.1%	59.0%	94.9%	-0.31
<i>In.inf</i> Faye	0.37	0.15	0.33	42.0%	90.0%	31.6%	15.4%	29.4%	48.8%	93.0%	-0.48
<i>Str.de</i> Sil	0.35	0.18	0.35	51.7%	100.0%	30.5%	13.4%	30.5%	44.0%	100.0%	-0.48
<i>Hl.uni</i> Sil	0.78	0.71	0.58	90.7%	74.7%	61.5%	56.3%	49.0%	91.5%	79.7%	0.16
<i>Lt.acu</i> Har	0.33	0.19	0.31	57.7%	96.2%	31.3%	18.8%	30.0%	60.0%	96.0%	-0.38
<i>Str.pl</i> Lib	0.66	0.53	0.55	80.0%	84.0%	47.4%	36.8%	42.1%	77.8%	88.9%	-0.04
<i>Raf.al</i> Lib	1.42	1.42	0.76	100.0%	53.5%	66.0%	66.0%	46.0%	100.0%	69.7%	0.46
<i>Lt.rcd</i> Wayn	0.37	0.26	0.36	70.3%	97.3%	37.0%	26.0%	36.0%	70.3%	97.3%	-0.27
<i>Raf.al</i> Fair	0.82	0.79	0.30	96.0%	36.0%	54.1%	52.5%	27.9%	97.0%	51.5%	0.60
<i>Oe.lir</i> Dec	0.67	0.62	0.33	92.9%	50.0%	52.4%	47.6%	33.3%	90.9%	63.6%	0.43
<i>Oe.ing</i> Dec	0.60	0.40	0.52	66.7%	86.7%	44.0%	28.0%	36.0%	63.6%	81.8%	-0.20

Table 1.3. Pearson's product moment correlation coefficients and p-values between the single-valve repair frequencies and true repair frequencies of all samples. Single-valve repair frequencies were calculated using the dorsal or ventral valve only or by using the valve (dorsal or ventral) with the greatest number of repairs for each sample.

		Valve		
		Dorsal	Ventral	Greatest
Rr	rho	0.983	0.795	0.995
	p-value	< 0.001	< 0.001	< 0.001
%R	rho	0.946	0.846	0.989
	p-value	< 0.001	< 0.001	< 0.001

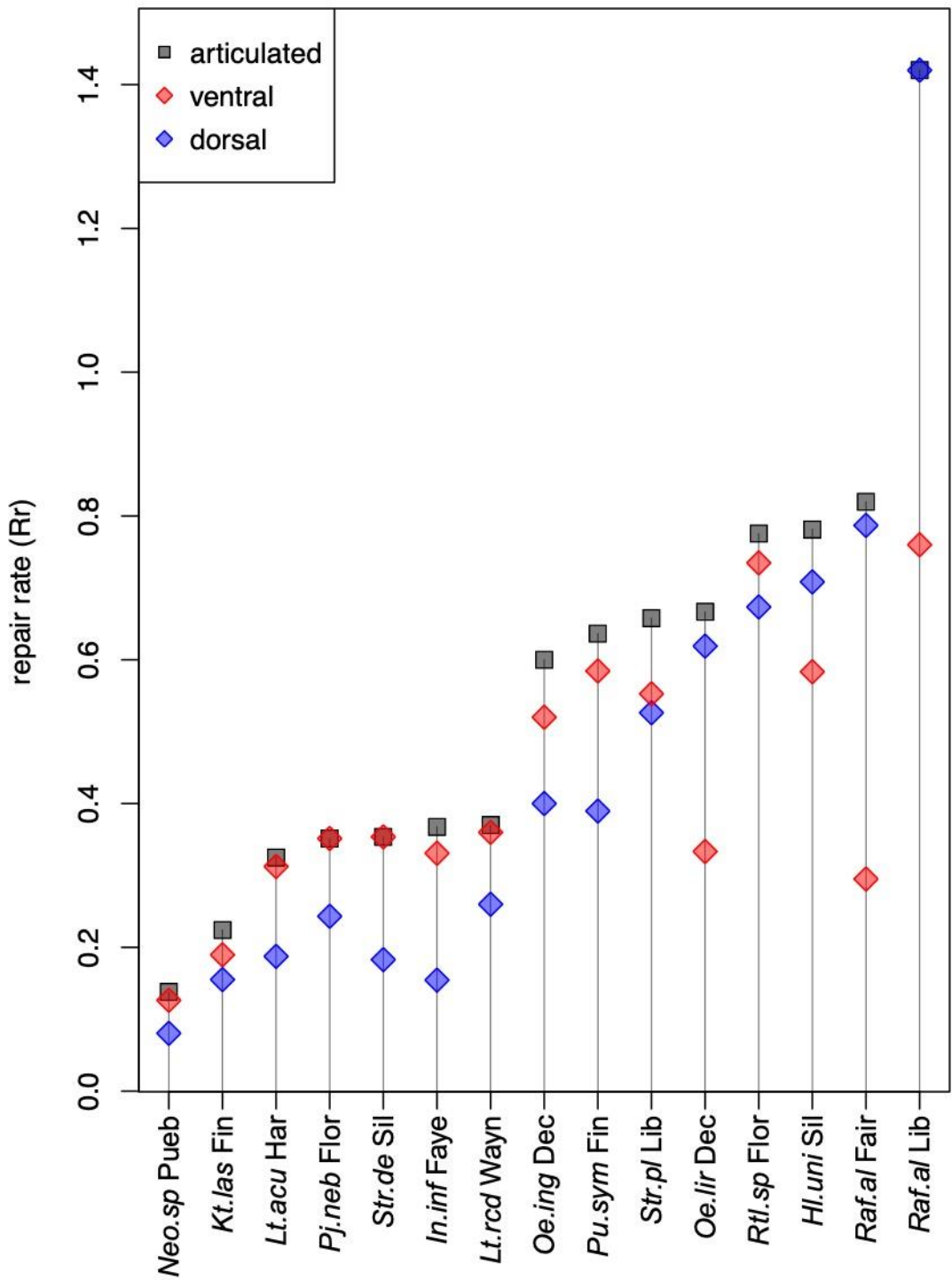


Figure 1.1. Bead plot showing the articulated repair rate compared to the single-valve repair rates ordered left to right by increasing Rr.

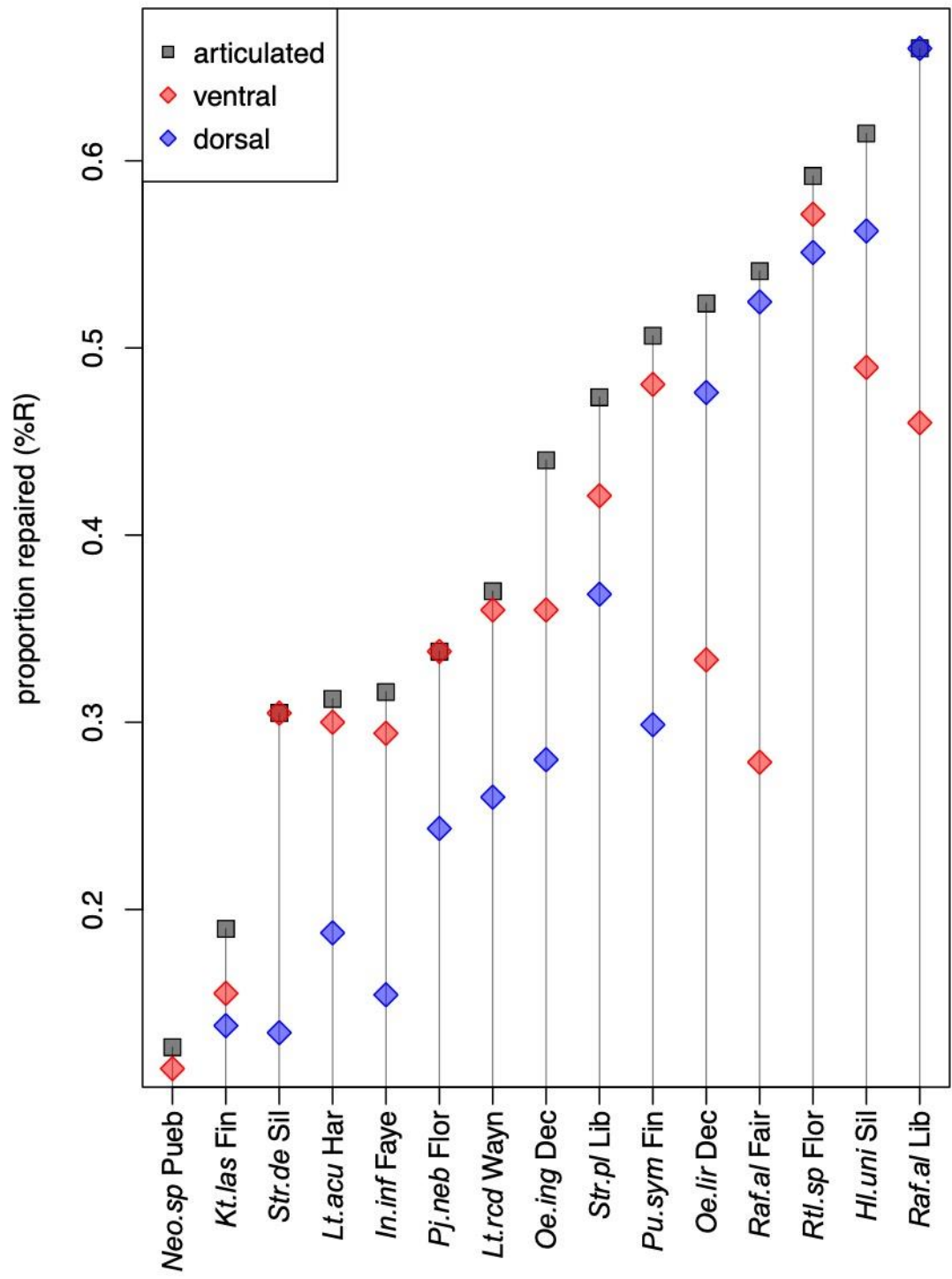


Figure 1.2. Bead plot showing the articulated %R values compared to the simulated valve-specific %R values ordered left to right by increasing articulated %R.

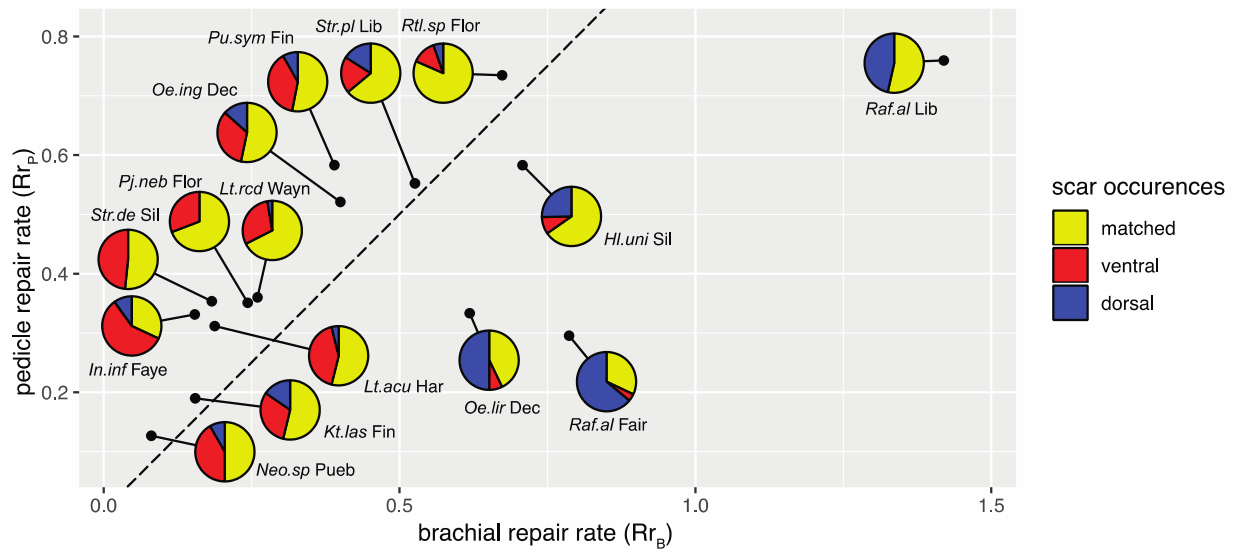


Figure 1.3. Scatterplot of valve specific Rr values and pie charts showing the relative abundance of scar occurrences on each valve (dorsal, ventral, or matched) in each sample. The dotted line represents the case in which the valves show the same Rr value. Samples to the right/below the line have higher Rr values on the dorsal valve while samples to the left/above the line have higher Rr on the ventral valve.

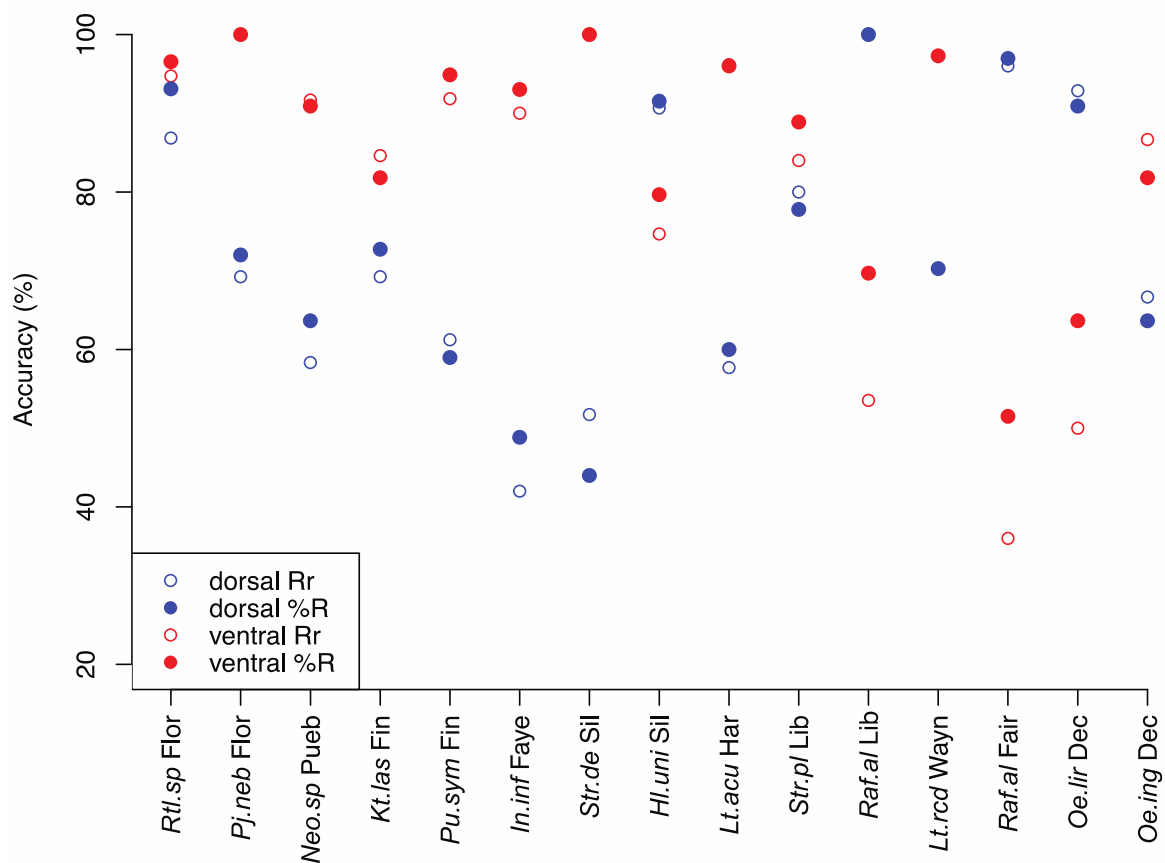


Figure 1.4. Valve accuracy of single valves for Rr and %R. The closer the proportion is to 100%, the more accurate the valve specific repair frequency. Rr measurements are the number of scars represented by one valve as a percent of the total number of scars in the assemblage, while %R measurements are the number of scarred valves (dorsal or ventral) as a percent of the total number of articulated scarred individuals with at least one scar.

2 Chapter 2

Intrinsic factors affecting predator success in crab-gastropod encounters and their implications for repair frequencies

2.1 Introduction

Predation is an important force in shallow marine ecosystems, affecting community structure and spatial organization (Schindler et al., 1994; Stafford et al., 2015b; Yamada and Boulding, 1996). Unsuccessful predation has the potential to provide considerable information when failed attacks result in observable deformities or evidence of injury on prey. For example, in marine ecosystems, gastropods often repair damage to their shells caused by failed predation. This repaired damage leaves characteristic scars (repair scars, Fig. 2.1) that permanently record predator-prey encounters (Kowalewski, 2002; Leighton et al., 2013; Schindel et al., 1982; Stafford et al., 2015a; Vermeij, 1982b, 1982a). As gastropod shells grow by accretion, these repair scars provide long-term records of predation over the lifespan of the prey, which can be several decades for some species (Schoener, 1979; Tyler et al., 2019; Vermeij, 1982a). Recent study has shown that because of this, patterns of repair frequency are buffered against short-term perturbations such as seasonal changes or ephemeral environmental and climatic disturbances (Tyler et al., 2019). Due to the importance of predator-prey encounters in these ecosystems, temperate intertidal crab-gastropod predator-prey systems have become a model for examining predation and testing the utility of repair scars as a proxy for predation intensity (e.g., Boulding et al., 1999; Cannicci et al., 2007; Dietl and Alexander, 1998, 2009; Geller, 1983, 1982; Molinaro et al., 2014; Ray-Culp et al., 1999; Schindler et al., 1994; Stafford et al., 2015b; Tyler et al., 2019; Yamada and Boulding, 1998, 1996). However, as repair frequency can be associated not only with encounter rate but also with predator success/failure, understanding how single

encounters scale to population level repair frequencies requires a detailed understanding of which factors affect predator success or failure in an individual encounter. To consider the potential for repair, we must first determine the causes of failure. Thus, the present study employs arena experiments to test the influence of specific factors –predator size, prey size, and prey species – on success and failure in encounters between species commonly employed in modern repair scar studies: the predatory red rock crab *Cancer productus* (Cancridae; Randall, Fig. 2.2), and two of its common gastropod prey, the striped dog-whelk, *Nucella ostrina* (Muricidae; Deshayes, Fig. 2.3), and the black turban snail, *Tegula funebris* (Tegulidae; Adams, Fig. 2.3).

The relationship between individual crab-gastropod encounters and population-level repair frequency is poorly understood in part because repair scars are failed attacks; repair frequency is a measure of unsuccessful encounters in a population rather than absolute mortality. Successful encounters typically cannot be determined without direct observations, as successful predation, especially in the case of durophagous predation, usually destroys/fragments the prey shell (but see Leighton et al., 2016). There is a growing body of evidence that spatial patterns in repair frequencies of a single prey species are largely a function of crab density (Boulding et al., 1999; Molinaro et al., 2014b; Schindler et al., 1994; Stafford et al., 2015b; Tyler et al., 2019; Yamada and Boulding, 1998), and thus correspond with attack frequency. However, as repair scars are the result of unsuccessful crab-gastropod encounters, repair frequencies in a population are not only a product of the frequency of predator-prey encounters, but also of the success rate of the crab (the per-encounter likelihood of a predator successfully killing its prey). For example, a shell-crushing predator with a high success rate would kill its prey while leaving few repair scars. In contrast, an inefficient predator with a low success rate would be unlikely to kill its prey

and would leave many repair scars leading to high repair frequencies. Similarly, differences in shell strength or behaviour between prey species might influence predator success. Thus, while spatial variation in predator density would be expected to affect repair frequency within a single prey species, variation in repair frequency between prey species might be more influenced by the characteristics of those prey species and the effects of those characteristics on prey survival.

For any given encounter, the likelihood of predator success is dependent on intrinsic and extrinsic factors. Intrinsic factors include physical and behavioural properties of the predator and prey such as predator strength and prey defenses. Generally, larger predators will have a greater likelihood of killing prey than smaller predators, whereas larger prey are more likely to survive a predatory encounter than small prey (Zipser and Vermeij, 1978). Intrinsic factors also include attributes of predator and prey species which are typically correlated with size such as relative crushing strength of the predator and prey shell thickness (Schindler et al., 1994; Stafford et al., 2015b; Stafford and Leighton, 2011; Vermeij, 1982a, 1977). In addition, the identity of the predator and prey species is itself an important factor; prey gastropod species differ in shape, shell mineralogy, shell structure, and behaviour, all of which could potentially affect the outcome of an encounter (Barclay et al., 2019). For example, shell strength can be dependent on the material of which shells are made, and can vary between different shell morphologies (Currey, 1988).

Intrinsic factors – such as predator and prey identity and size – not only may influence the likelihood of predator success but also may affect the duration of the encounter. The longer the encounter, the larger the temporal window in which an extrinsic factor (e.g., the predator's competitors or predators or physical disturbances) might interrupt and alter the outcome. If crabs can kill and consume prey quickly, there is a very small temporal window during which extrinsic

factors may come into play. However, if there is a large temporal window, it is much more likely that an encounter's likelihood of success could be influenced by the product of extrinsic factors. Thus, intrinsic factors, such as crab and gastropod species and size, might not only affect predator success directly, but could also potentially affect success rates indirectly through the duration of the encounter. To understand the possible influence of extrinsic factors on success rates and repair frequencies, we must first determine the normal expectation for the length of a predator-prey encounter, based solely on intrinsic factors. Therefore, here we evaluate not only how intrinsic factors affect the likelihood of success but also how intrinsic factors affect the duration of encounters. Specifically, we measure the amount of time required for the crab to break the prey's shell and begin consumption (grappling time) and the total amount of time required to kill and consume the prey (handling time).

While both *T. funebris* and *N. ostrina* are common in rocky and cobble intertidal environments, they are only distantly related, and have contrasting shell compositions, morphologies, and lifestyles. *T. funebris* has a globose, squat shell made of nacre (columnar stacks of aragonite crystals) (Geller, 1982) with a relatively small and circular aperture (Fig. 2.3). In contrast, *N. ostrina* has a thinner, more elongate high spired shell made of an outer layer of calcium carbonate and an inner layer of cross-lamellar aragonite (Avery and Etter, 2006; Watabe, 1988) with an elongate aperture.

Cancer productus is one of the most common intertidal durophagous predators along the west coast of North America and is known to consume *N. ostrina* and *T. funebris* frequently (Molinaro et al., 2014; Stafford et al., 2015b). As is typical for most cancrid crabs, *C. productus*' chelae are only weakly dimorphic (Vermeij, 1977; Yamada and Boulding, 1998; Zipser and Vermeij, 1978). This is characteristic of generalist durophagous crabs (Zipser and Vermeij,

1978). Cancrids have been observed to utilize both crushing (prey crushed outright) and peeling (peeling back the aperture to get at soft tissue) to break into gastropods, often switching strategies rapidly without apparent preference for either (Lawton and Hughes, 1985; Zipser and Vermeij, 1978). Although not as specialized for a particular attack strategy as are many tropical species, *C. productus* is still quite strong (Yamada and Boulding, 1998); adults have been recorded producing over 200 N with their chelae (Taylor et al., 2000).

T. funebris and *N. ostrina* co-occur in close proximity throughout much of their ranges and are common prey items for *C. productus*. Although the two species inhabit overlapping intertidal zones and are of comparable size in most instances, one previous study (Tyler et al., 2015), observed that *N. ostrina* has lower repair frequencies than *T. funebris*. These differences in repair frequencies could be due to attack frequency, in which case *C. productus* may prefer *T. funebris* or have less access to *N. ostrina* due to the latter's slightly higher position in the intertidal. Alternatively, higher repair frequencies on one species may result from higher survival rates of that species. If variation in repair frequencies between these species is due to differences in predator success rates, *N. ostrina* should have a much lower likelihood of survival in encounters with *C. productus* relative to *T. funebris*.

Using arena feeding trials with the crab *C. productus*, and the two prey gastropods *T. funebris* and *N. ostrina*, we test the following hypotheses: (1) Predator success rates between the two prey species will differ. (2) Grappling and handling times between the two gastropod prey species will be different. (3) Predator success rates will increase with crab chela size. (4) Predator success rates will decrease with increasing gastropod size. (5) Grappling and handling times will decrease with increasing crab chela size. (6) Grappling and handling times will increase with increasing gastropod size. Experimental results were then compared with repair

frequencies from three populations of co-occurring *T. funebris* and *N. ostrina* in British Columbia (Canada). If predator success rates vary between gastropod species and have an effect on repair frequencies measured in natural systems, then the prey species more likely to survive encounters with *C. productus* should have greater repair frequencies.

2.2 Methods

2.2.1 Materials

To examine potential factors contributing to the likelihood of predator success or failure, and by extension, the potential for repair scar formation, we conducted predator-prey arena experiments using the gastropods *T. funebris* and *N. ostrina*, and their common predator, *C. productus* (Figs. 2.2, 3.3). These taxa were selected because they have been used in studies on repair frequency that have demonstrated the use of repair scars as a proxy for attack frequency (Molinaro et al., 2014b; Stafford et al., 2015b; Tyler et al., 2015). In addition, these three organisms co-inhabit a broad geographic range in the intertidal of the northeastern Pacific, ranging from southern Alaska to California (Marko et al., 2003; Paine, 1969; Yamada and Boulding, 1998). We used arena experiments as they allow observation and measurement of intrinsic factors likely to affect predator success and they potentially can determine how differences in predator and prey attributes may translate mechanically into differences in predator success rates.

2.2.2 Collection and trials

T. funebris and *N. ostrina* were collected from Bodega Marine Reserve and Carmel Beach near Bodega Bay. The maximum dimension of each gastropod was used as a proxy for prey size. Generally, for a given species, larger shells are stronger than smaller shells (Barclay et al., 2019; Currey, 1988; Lawton and Hughes, 1985; Schindler et al., 1994; Yamada and

Boulding, 1998; Zipser and Vermeij, 1978). The maximum dimension of *T. funebris* was measured as the width of the shell from the aperture lip to the opposing point on the last body whorl. The maximum dimension of *N. ostrina* was measured as the height of the shell from the distal edge of the siphonal canal to the apex. Snails were marked with numbers and symbols on their body whorl so that they could be uniquely identified during feeding trials. Sets of five *T. funebris* and five *N. ostrina* with the same mean variance in size $\pm 5\%$ were used in each experimental trial.

C. productus were collected from Bodega Bay, California, USA by the Aquatic Resources Group of Bodega Marine Laboratory (University of California, Davis). The 18 crabs in the study had carapace widths ranging from 86.9 mm to 121.4 mm with chelae heights ranging from 18.16 mm to 30.11 mm. Dominant (larger) chela height, measured as the minimum distance between the dorsal intersection of the dactylus and manus and the base of the propodus of the chela using digital calipers (± 0.01 mm), is used here as a proxy for predator size. Chela height is proportional to the cross-sectional area of the closer muscle bundle responsible for crushing, and is correlated with the relative strength of the predator (Abele et al., 1981; Vermeij, 1977; Yamada and Boulding, 1998), independent of differences due to gender (Yamada and Groth, 2016). More females than males were used due to their greater occurrence in traps at the size range considered by this study. Crabs with strongly dimorphic claws were not used because such claws in cancrids are likely indicative of previous injury or loss of the limb (Vermeij, 1977; Yamada and Boulding, 1998). Crabs were marked after collection using paint pens and were starved for a minimum of three days prior to their individual trials to equalize hunger. Each crab was used in a minimum of two trials though they did not always feed during a trial.

Feeding trials were conducted between June 1st and 21st of 2017 in tanks ~ 25 cm wide by 50 cm long with a depth of approximately 35 cm (Fig. 2.4) with running seawater at a temperature of ~ 12°C. Trials were performed at night, under red light to minimize disturbance, as crabs see poorly at the red end of the light spectrum (Cronin and Forward, 1988). A set of five *T. funebris* and five *N. ostrina* were evenly distributed across a rock and given time to attach prior to introduction to a tank with a predator. After placing the crab in the tank, the rock with the attached gastropods was placed on the opposite side of the tank. Trials were then monitored for 45 minutes to give crabs sufficient time to acclimate and attack the gastropods (supplementary video). If a crab did not attempt to kill a gastropod within this time, it was returned to its holding tank before inclusion in a subsequent trial within the next 48 hours. In successful feeding trials, crab and gastropod encounters were recorded until crabs stopped attempting to take prey for 30 minutes, at which point the trial was concluded. Trials typically lasted 1.5 to 4 hours.

In a natural setting, duration of the predator-prey encounter could affect the success or failure of the attack; the longer the duration, the greater the likelihood that a competitor or the crab's own predators might interfere causing the crab to abandon the prey. In this way, prey which take longer to kill would likely have a greater chance of survival in natural systems when the amount of time a crab has to kill a prey item is limited. Weak shells are likely to be instantly crushed, but stronger shells, either due to material or architectural strength, may take more time to break or force the crab to resort to peeling which may take more time. Thus, we examined not only the outcome of each encounter, but also the duration. In each crab-snail encounter, both grappling and handling time were recorded. Grappling time was recorded as the time from the start of the encounter until consumption had begun or, in cases where consumption did not occur,

when the crab dropped the snail. Consumption was defined as beginning when the crab was able to remove the operculum of the prey, or when the shell of the prey was damaged in a manner that allowed the crab to access exposed soft tissue. Handling time was defined as the total duration of the encounter until the end of consumption and did not include digestion. The end of consumption was defined as when the crab dropped the remains of the deceased prey and resumed foraging or otherwise exploring the tank. In the case of encounters that did not end with consumption, the encounter was declared over when the predator was no longer in contact with the prey (i.e., if the crab immediately caught prey dropped beneath itself using its walking legs, the encounter was not concluded).

If the same snail was encountered multiple times in the same trial, only the attributes of the first encounters with each specific prey item were used. Subsequent encounters may be affected by the first encounter in unpredictable ways (i.e., due to shells being weakened by previous encounters or effects on the crabs' behaviour due to previous lack of success with specific specimens) and it is unknown how often re-encounters occur in natural systems.

Lastly, the method (crushing or peeling) by which the crab successfully gained entry to the shell and access to the soft tissue was recorded. It is well known how repair scars are generated in crab-gastropod encounters in a mechanical sense from direct observation in previous studies (Bertness et al., 1981; Zipser and Vermeij, 1978). Generally, most crabs will first try to crush their prey and, if unsuccessful, will then try to "peel" open spirally-coiled gastropods by inserting their propodus (manus) into the snail aperture and pulling back on the lip of the aperture (Bertness and Cunningham, 1981; Zipser and Vermeij, 1978, Fig. 2.2). These 'peels' leave distinctive v-shaped damage which may be repaired, producing characteristic scars should the prey survive (Stafford et al., 2015a, Fig.2.1). This crush-then-peel strategy is

employed by most generalist crabs, such as cancrids, though some specialized crabs might use other methods or rely on crushes or peels exclusively (Zipser and Vermeij, 1978). Crushing was defined as the crab gripping the prey, typically across the spire, and attempting to crush the shell outright. Peeling was defined as any strategy that involved placing any part of the chelae within the prey's aperture in order to chip away at the outer margin until the prey shell had been peeled back enough that the crab could reach the soft tissue and begin consumption. In the case of crabs which are known to switch between crushing and peeling strategies such as *C. productus*, it is generally thought that peeling occurs when the crab is unable to crush the prey (Zipser and Vermeij, 1978). As crushing can be nearly instantaneous, a shell that cannot be crushed would require much more time to kill than a shell which can be crushed (Barclay et al., in review). This could indirectly decrease the likelihood of success in a wild encounter as the period of time crabs have can be limited by interruptions from extrinsic influences such as wave energy, predators, or competitors. Thus, while both crushes and peels can result in encounters in these arena experiments, it is important to understand if certain prey are more likely to be crushed or peeled and to determine if one strategy takes more time than the other.

2.2.3 Repair frequencies

If intrinsic factors result in differential prey survival in the experimental trials, repair frequencies should similarly differ in natural settings, resulting in greater repair frequencies for the better defended species. Therefore, *T. funebris* and *N. ostrina* repair frequencies were examined at three localities in rocky intertidal habitats on Vancouver Island in British Columbia (Canada) near the Bamfield Marine Sciences Centre over two field seasons (2009 and 2010). Some of the *T. funebris* data were previously presented in an unrelated study (Stafford et al., 2015b).

Repair frequencies of west coast *T. funebris* populations have often been correlated with crab abundance (Molinaro et al., 2014b; Stafford et al., 2015b; Tyler et al., 2019), which suggests that variation in repairs on this single species is driven primarily by attack frequency. However, most studies examining repair frequencies have focused on one prey species, and it is unclear how differences between cooccurring prey species would affect prey survival and repair frequencies. To address this question both gastropod species were surveyed from three field sites: Dixon Island (48°51'12.5" N, 125°07'19.3" W), Scott's Bay (48°50'04.6" N, 125°08'48.3" W) and Brady's Beach (48°49'36.1" N, 125°09'17.6" W). All three sites are wave-exposed, facing the open water of Barkley Sound with mean maximum daily wave velocities of approximately 1.75, 1.85, and 5.0 m/s⁻¹ respectively (Bates et al., 2009; Neufeld and Palmer, 2008).

At each locality a minimum of 50 live, "adult" (at least three whorls) individuals per species were examined for repair scars and then immediately returned unharmed to their resting place in the field. Similar to previous studies and recommendations (Alexander and Dietl, 2003; Kowalewski, 2002; Leighton, 2001), repair frequency was calculated in two ways: First, we divided the number of individuals with at least one repair scar by the total number of individuals, which is the proportion repaired, %R (RF1 of Molinaro et al. 2013), the proportion of individual prey in the sample that were attacked at least once and survived. Second, we divided the total number of scars by the total number of individuals, which is the repair ratio, RR (RF2 of Molinaro et al., 2013), the ratio of scars to individuals in a sample. We compared the repair frequencies of the two species at each locality with any predictions developed from the arena experiments, i.e., if one prey species was more likely than the other prey species to survive a

crab attack in the arena, we expected that the same species would have greater repair frequencies in the field.

2.2.4 *Statistical analysis*

Regression methods were used to determine if the strategy of attack (crush or peel), likelihood of success, and duration of encounters differed significantly between *T. funebris* and *N. ostrina* encounters. For each of the dependent variables, a model consisting of prey species and crab identity was compared to a model including only crab identity using log ratio test. If the models for each dependent variable were significantly different and the model including prey species had a lower AIC value, this would indicate that prey species (*T. funebris* or *N. ostrina*) had a significant effect on the dependent variable. Binomial logistic models were used to model strategy of attack and likelihood of success while generalized linear models were used to model handling and grappling times.

Regression methods were also used to determine if the dependent variables likelihood of success, grappling time, and handling time were dependent on the independent variables prey size, predator size, and attempt number (the order at which crabs attempted to kill prey in each trial, inclusive of encounters with both species of gastropod). Only first encounters were used for these models so that encounters were independent from previous attempts by the crab to break into the prey item. In each case, models were performed for both snail species separately. Likelihood of success (i.e., the predator kills the prey) for an encounter and which strategy (crush or peel) is employed by the crab, were modeled separately for each gastropod species using binomial logistic regression. Grappling and handling time were modeled for each gastropod species separately using generalized linear models; only successful encounters were included

because the objective of the model was to determine when and under what conditions shell failure occurs.

To determine which independent variables contributed significantly to the fit of the models, we chose the most parsimonious model of the set of models derived from all combinations of independent variables for each dependent variable according to its AIC score. AIC scores reflect the fit of the model relative to the number of variables, with lower AIC scores indicating a better fit. AIC scores penalize models with more variables and therefore help avoid including variables that do not significantly increase the goodness of fit of the model. We then compared the most parsimonious model to the sub-optimal models, using log-likelihood ratio tests. This test compares the goodness of fit of two different models to test if one model is a significantly better fit than the other according to their likelihood as calculated by log-likelihood. A significant result indicates that the model with a lower AIC score is a significantly better fit than the other model whereas a nonsignificant result indicates that the added or dropped variable did not significantly change the fit of the model. We also performed a log-likelihood ratio test to determine if the most parsimonious model differed significantly from a null, intercept-only model (i.e., a model with no independent variables and no slope). If an independent variable is included within the most parsimonious model and that model is significantly different from the null intercept model, then this independent variable has a significant effect on the dependent variable within the model. All analyses and models were performed in R (version 3.5.2, R Core Team, 2018).

2.3 Results

2.3.1 Trial outcomes

Of the 60 feeding trials conducted, 30 involved successful or attempted consumption by the crabs, resulting in a total of 179 unique predator-prey encounters. This consisted of 99 *T. funebris* and 80 *N. ostrina* encounters. Crabs were much less successful in encounters with *T. funebris* than with *N. ostrina* (55% and 92% of encounters respectively, log-ratio test, $p = 0.004$). Crabs also had significantly greater grappling and handling times in encounters with *T. funebris* (467 s and 1036 s respectively) than in encounters with *N. ostrina* (means = 170 s and 498 s, $t = -4.92$, log-ratio test, $p < 0.001$ for both tests).

2.3.2 Modeling results – success rate

In *T. funebris* encounters, larger predators were more likely to be successful. Furthermore, all crabs were less likely to be successful as they encountered more prey. This was shown in the most parsimonious model; claw size increased the likelihood of success while increasing attempt number decreased the likelihood of success (Table 2.1). This model was significantly different from a null (intercept-only) model; however, adding attempt number and removing prey size led to less parsimonious models that were not significantly worse fits. Only removing prey size resulted in a significantly less parsimonious fit ($p < 0.05$). Success rate was not modelled with *N. ostrina* encounters because there were not enough failed encounters to build a model.

2.3.3 Modeling results – crab strategy

For *N. ostrina*, encounters between large predators and small prey were more likely to result in crushes while encounters between small predators and large prey were more likely to result in peels. Claw size and prey size were both significant predictors of strategy (crush or

peel) and excluding them resulted in a significantly less parsimonious model ($p < 0.05$). Adding attempt number resulted in a less parsimonious model that was not a significantly different fit. Except for a single encounter, all encounters with *T. funebris* resulted in peels, so strategy in *T. funebris* encounters was not modelled.

2.3.4 Modeling results – grappling time

The crabs' grappling times increased with increasing prey size in successful encounters with *T. funebris* (Table 2.1, Fig 2.5). The most parsimonious model for grappling time included prey size alone and was significantly different than a null model ($p < 0.05$). Adding attempt number and/or prey size decreased the fit of the model though not enough to be significant.

Grappling time in *N. ostrina* encounters increased with increasing prey size and decreasing claw size. The most parsimonious model included both prey size and predator size though it was not significantly different from a null model ($p = 0.10$). The addition of attempt number resulted in a less but not significantly less parsimonious model.

2.3.5 Modeling results –handling time

Handling times in both *T. funebris* and *N. ostrina* encounters increased with increased prey size and decreased with increasing predator size (Table 2.1, Fig 2.5). For both species of snail, the most parsimonious model of handling time included both prey and predator size. Also, for both species of snail, excluding claw size resulted in a significantly less parsimonious model (*T. funebris*, $p < 0.005$; *N. ostrina* $p \ll 0.005$). Similarly, the exclusion of prey size also led to less parsimonious models for both prey species but the difference in fit was only significant in *N. ostrina* encounters ($p \ll 0.05$). The addition of attempt number resulted in a less but not

significantly less parsimonious model for both species of snail. The most parsimonious model was significantly different from a null model for both species of snail ($p < 0.005$).

2.3.6 *Behavioural observations*

Crabs employed two discrete methods of preying upon gastropods: crushing and peeling. Crabs were observed grasping a gastropod by the lip of its aperture with one chela and attempting to crush the gastropod shell across the spire with the other chela. Peeling involved either gripping and flexing the margin of the gastropod's aperture with both chelae or by gripping and flexing the apertural lip outwards with one chela while the other was partially inside the shell gripping the columella. While it was easy to determine when the crabs were trying to peel shells (i.e., Fig. 2.2), it was difficult to determine if the crab was attempting to crush the shell or just handling the shell. Strategy at the time of shell failure, when consumption began, was recorded as it would be apparent at that point whether the crab had been crushed (catastrophic failure) or peeled (incremental peeling along the outer margin of the shell and eventual removal of the operculum). Typically, crabs would alternate between crushing and peeling, and when peeling, would switch back and forth between both methods of peeling. In addition, when peeling, crabs would often reorient the gastropod shell by using their mouthparts in combination with their chelae and walking legs. This almost always involved a switch in handedness (i.e., which chela was gripping the lip of the aperture and which was gripping the columella or a reversal of the direction of shear when both chelae are on the apertural lip). Unsuccessful peeling attacks resulted in v-shaped damage or chipping near the aperture; this damage would result in distinctive repair scars over time (Fig. 2.1). Successful peeling attacks typically resulted in damage which removed most of the body whorl, leaving only the spire, where whorls are densely packed, intact. Crabs more commonly peeled, regardless of prey

species, but crushing was much more frequently employed in successful attacks of *N. ostrina* (26%) than in those of *T. funebris* (2.3%) (log-ratio, $p < 0.001$).

T. funebris and *N. ostrina* exhibited different behaviour during the trials. *T. funebris* was highly mobile, which often resulted in individuals leaving the rock, crossing the arena and even climbing up the vertical side walls of the tank. However, the direction of travel was not always away from the crab. Although *T. funebris* was always moving, individuals became more active when conspecifics were crushed, though this was not explicitly tested. In contrast, *N. ostrina*, though occasionally mobile, more often remained stationary with their apertures flush against the rock. It was apparent that *C. productus* had greater difficulty removing *N. ostrina* from the rock than *T. funebris*, often requiring the crabs to brace themselves and pry with both chelae to remove *N. ostrina*. However, this still did not prevent crabs from relatively quickly detaching *N. ostrina* from the substrate; we observed no cases in which the crab failed to remove the gastropod.

2.3.7 Repair frequencies

At each of the three field sites, repair frequencies were greater for *T. funebris* than for *N. ostrina* (Table 2.2). This was true for both %R and RR. Repair frequencies varied within a species across localities but were always greater for *T. funebris* within each locality.

2.4 Discussion

2.4.1 Differential prey survival

In experimental trials, crabs were less likely to succeed in encounters with *T. funebris* than encounters with *N. ostrina*, and *T. funebris* was significantly more resistant to both crushing and peeling attacks. Crabs succeeded against *T. funebris* in only 55% of encounters,

compared to 92.5% against *N. ostrina* repair frequencies. The difference in success rates between *N. ostrina* and *T. funebris* is likely due to intrinsic factors, such as differences in shell strength and morphology. When crushing the shell of *N. ostrina*, the crab would do so by gripping the shell across the spire. This tactic, however, is not possible with *T. funebris* because of their shell's globose shape and smooth shell surface. When attempting to crush *T. funebris*, the chelae would almost inevitably slide off the shell, much like trying to handle a ball bearing with scissors. This makes it much harder for the crab to apply force perpendicular to the columella and often results in the crab attempting to crush sub-parallel to the columella. Without the elongate conical spire, there is no easy way for a crab to grip and crush *T. funebris* reliably. Crabs would usually handle *T. funebris* using their chela in conjunction with their mouth parts and walking legs. It was only possible for crabs to hold the globose *T. funebris* using chelae alone by grabbing the lip of the aperture, in which case, crushing the shell would not be possible. This difficulty with handling increases the chance of the snail surviving the encounter by being accidentally dropped (which we observed frequently) and forces the crab to switch to peeling, probably increasing the duration of the encounter. Other gastropods with similar squat trochiform and smooth shells have been found to have higher repair frequencies than those with high spired shells in both modern (Cadée et al., 1997; Schmidt, 1989) and fossil studies (Leighton et al., 2013; Schindel et al., 1982).

2.4.2 *Predator success rate*

In encounters with *T. funebris*, larger crabs were more likely to be successful (Table 1.1). Additionally, crabs were less likely to be successful after more encounters during the trial (Table 2.1). Thus, larger crabs had higher per encounter success rates than small crabs, and success was highly dependent on the crab's previous encounters during the trial. The finding that

crabs were less likely to succeed in subsequent encounters suggests that the likelihood of success may also in part be tied to variables such as hunger and fatigue. This pattern of decreasing success with consecutive encounters could also result from crabs choosing smaller prey at the beginning of the experiment, which were easier to kill, and attacking the remaining prey which were harder to kill near the end of the trial. It has been found in other studies that crabs generally will select smaller prey than expected (Juanes and Hartwick, 1990). However, if an increase in prey size with consecutive encounters were responsible for the decrease in likelihood of success over the duration of the trial, it would be expected that there should be a correlation between prey size and the order of prey encountered, but there was none (Spearman's rank, $\rho = 0.0703$, $p = 0.49$).

2.4.3 Handling and grappling time

While handling and grappling times in encounters with both snail species were positively correlated with prey size and negatively correlated with predator size, there was a great difference in encounter duration between prey species (Fig. 2.5). The difference in handling times was so great that, on average, it would have been possible for a crab to have consumed multiple similarly sized *N. ostrina* (mean = 498 s) within the time required to kill and consume one *T. funebris* (mean = 1035 s). Longer handling times would increase the likelihood of extrinsic factors in natural settings, such as interruption by competitors, predators, or environmental factors such as passing waves. Failures due to interruption of big prey-small crab encounters may be further amplified in natural systems because smaller crabs are more likely to hide (Robles et al., 1989) and therefore more likely to be affected by their surroundings than their larger conspecifics. Thus, it is likely that natural encounters between relatively small predators and large prey, especially in the case of *T. funebris*, more commonly result in

survival of the prey, and thereby generation of repair scars, than observed in these arena experiments. Although we observed low success rates for small crabs in this study, their success may be even lower in natural settings due to the additional time required by small crabs to kill their prey (Figs. 2.1, 2.2). Considering the greater time required to kill *T. funebris* in comparison with *N. ostrina*, the difference in success rate between attacks of *T. funebris* and *N. ostrina* is likely conservative in our study and may be greater in their natural setting.

Prey size was an important variable for predicting grappling and handling times but did not significantly affect the likelihood of a crab being successful in an encounter. Stafford et al. (2015b) found prey size to be a contributing, though not dominant, factor affecting repair frequencies on *T. funebris*. The lack of contribution of shell size in our models could be because the size range of *T. funebris* considered by this study was not great enough to contribute significant variance to the model in comparison to the in-situ populations from British Columbia considered by Stafford et al. (2015b) which had greater maximum shell size than the California population sampled for the present study. However, considering that prey size did have an effect on grappling time, an alternative explanation is that prey size can indirectly affect success rates in the natural systems. Given that larger prey requires more time to kill, it could be that prey size can affect attack frequency by increasing the chance for interruption of the encounter by extrinsic factors such as wave energy, competing conspecifics, and other predators from a higher trophic level. This could lead to prey size having a greater effect on success rate in field studies than in arena experiments due to long handling times and interruption. However, prey size has not been a significant predictor of repair frequencies thus far for these specific taxa (Stafford et al., 2015b), instead predator density, and thus encounter frequency, is correlated with repair frequency (Molinaro et al., 2014b; Stafford et al., 2015b; Tyler et al., 2019).

2.4.4 Prey behaviour

N. ostrina typically were immobile with their aperture flush with the rock's surface for the duration of the trials. In the less common cases in which *N. ostrina* fled, they invariably climbed under the rock. In contrast, *T. funebris*, is known to flee (Bullock, 1953; Geller, 1982) and escape tidepools (Jellison et al., 2016) when detecting predators, may have been disadvantaged by the enclosed arena and lack of refuge. *T. funebris* was often found by crabs when leaving the rock. While prey responses were not measured quantitatively, it was evident that *N. ostrina* spent most of its time in the trials withdrawn within its shell only moving towards the end of the trial. *N. ostrina* is known to flee when exposed cues from injured conspecifics and have a delayed flee response when exposed to *C. productus* cues (Mach and Bourdeau, 2011) but not to the extent observed in this experiment. It is likely that the prey's behaviour was modified by the close proximity and even physical contact by *C. productus*. Snails in our experiment were immobile but not truly withdrawn as they were still gripping the substrate, as evident from crabs struggling to remove that attached snails from the rock. With a low chance of survival once detected, it may be that *N. ostrina*'s best chance to survive is to remain stationary with the goal of avoiding detection and/or make it harder for the crab to remove it from the substrate. In contrast, *T. funebris*, having a higher chance of surviving an attack and being unable to attach to the substrate without exposing soft body parts, may benefit from risking detection in order to distance itself from the predator. Future studies on the differences in prey behaviour observed here would shed light on whether gastropod behavioral adaptations contribute to differential predator success rates in natural settings.

2.4.5 Predator behaviour

The arena experiments employed here also provide insight into how *C. productus* forages when there are multiple prey items of different species in very close proximity. Although experimental specimens were collected from localities that did not typically have the two prey species together in such close proximity at the great abundances employed in the experiments, *T. funebris* and *N. ostrina* populations, including those sampled in this study, do overlap. Crabs appeared to recognize a gastropod as prey during physical contact with a claw or walking leg and there did not seem to be selection of specific prey items by *C. productus*. Crabs typically attacked the first prey they encountered, consistent with observations by Barclay et al. (in review), and, while there were some short encounters, there were no instances of immediate rejection of prey.

2.4.6 Implications for repair frequencies

Given the great difference in predator success rate between encounters with different prey, *T. funebris* would be expected to have higher repair frequencies than *N. ostrina* because, in each crab-snail encounter, *T. funebris* would be more likely to survive and repair its shell, resulting in a repair scar, while *N. ostrina* would more likely be killed, resulting in the destruction of its shell. This hypothesis is corroborated by the repair frequencies observed at the three sites in British Columbia, where *T. funebris* repair frequencies were greater than *N. ostrina* repair frequencies at all localities. This is also consistent with repair frequencies reported by Tyler et al., (2015) in which *T. funebris* repair frequencies were greater than *N. ostrina* repair frequencies when the species co-occurred. Given that the predicted trend, that *N. ostrina* should have lower repair frequencies than *T. funebris* because of the higher predator success rates in *N. ostrina* encounters, is consistent with observed repair frequencies, this suggest that the

differences in repair frequencies between prey are likely attributed to differences in predator success.

The results of this study imply that repair scars, which scale with crab density in natural systems, primarily result from small crabs which have lower success rates than large crabs. Repair frequencies previously reported in the prey species considered here scale with crab abundance (i.e., Molinaro et al., 2014; Stafford et al., 2015b; Tyler et al., 2019) and not average crab size, which tends to be inverse to crab abundance in these systems (Robles et al., 1989). These trends show that the signal generated by small crabs (high rates of failure and thus repair) is not overwhelmed by the presence of large crabs: high energy sites with a low abundance of only small crabs still have lower repair frequencies than low in sites that have a greater abundance of both small and large crabs. While the differences in repair frequencies are primarily due to differences in encounter frequencies (Tyler et al., 2015), another contributing factor realized in this study may large handling times typical of small crab encounters. With large handling times, there is a greater chance of interruption of encounters by extrinsic factors that scale with crab abundance, such as competition or the presence of predators of crabs.

2.5 Conclusions

The great difference in the likelihood of success of *C. productus* between encounters with *T. funebris* and those with *N. ostrina* shows that a significant portion of variation in repair frequency between *T. funebris* and *N. ostrina* can be attributed to crabs being less successful in *T. funebris* encounters, especially in cases where *T. funebris* and *N. ostrina* populations coexist. Therefore, differences in repair frequencies between *T. funebris* and *N. ostrina* within the same localities are most likely due to differential survival from intrinsic factors, such as shell strength and shape.

Predator size had a direct effect on success rates for *T. funebris* encounters, but prey size did not. However, the long duration of encounters, which was affected by prey size suggests that in natural settings, extrinsic factors could potentially have large effects on success rate. Extrinsic factors (e.g., interspecific and intraspecific competition) tend to be greater in environments with a high abundance of crabs could be a contributing factor to high repair frequencies in these settings. While only predator size was found to contribute significantly to variation in success rates in *T. funebris* encounters, both predator and prey size had effects on grappling and handling times in both *T. funebris* and *N. ostrina* encounters. Therefore, predator and prey size may indirectly influence the outcome of encounters because extending handling and grappling times will increase the likelihood of interruption of encounters by extrinsic factors. Future research should examine if the variation in encounter duration introduced by predator and prey size is great enough to affect the likelihood of extrinsic factors changing the outcome of the encounter. The results of the present study illustrate the importance of both direct effects of intrinsic factors (differences in prey defenses influencing success) and indirect effects (prey defenses affecting grappling and handling time) on prey survival and ultimately, repair frequency.

Table 2.1. Results of binomial logistic regression and generalized mixed models. The outcome of each encounter, success or failure, and the strategy employed by crabs in successful using a binomial logistic regression. Grappling and handling time were modeled using generalized linear models. P-values were calculated using a log-ratio test between the most parsimonious model (denoted as the "reference" model) and less parsimonious models.

Model	Coefficients and standard error						AIC	ΔAIC	p
	Attempt	SE	Claw Size	SE	Prey Size	SE			
<i>Tegula funebris</i> - success vs failure (binomial logistic regression)									
Add prev. handle	-0.273	0.160	0.152	0.0774			137.1	-1.3	0.3892
Add prey size	-0.158	0.0838	0.126	0.0707	-0.0335	0.083	137.7	-1.9	0.6865
Reference	-0.160	0.0838	0.127	0.0708			135.8	0	NA
Drop claw size	-0.141	0.0817					137.3	-1.5	0.0621
Drop attempt			0.109	0.0679			137.7	-1.9	0.0492
Intercept model							138.4	-2.6	0.0371
<i>Nucella ostrina</i> - peel vs crush (binomial logistic regression)									
Add attempt	0.05637	0.107	-0.23714	0.10815	0.41729	0.18623	67.9	-1.7	0.595
Reference			-0.2361	0.1082	0.4217	0.1866	66.2	0	NA
Drop claw size					0.3611	0.1708	69.2	-3	0.0242
Drop prey size			-0.19788	0.09997			70.1	-3.9	0.015
Intercept model							72.2	-6	0.000381
<i>Tegula funebris</i> - grappling time (generalized linear model)									
Add attempt	3.20E-05	1.39E-04			-2.65E-04	1.32E-04	776.5	-2.2	0.816
Add claw size			1.08E-04	8.59E-05	-2.41E-04	1.37E-04	774.5	-0.2	0.185
Reference					-2.65E-04	1.33E-04	774.3	0	NA
Intercept model							776.5	-2.2	0.0401
<i>Nucella ostrina</i> - grappling time (generalized linear model)									
Add attempt	-0.043	0.0624	-0.0993	0.0618	0.151	0.1043	291.6	-1.5	0.491
Reference			-0.10006	0.06159	0.151	0.1039	290.1	0	NA
Drop prey size			-0.09707	0.06203			290.3	-0.2	0.145
Drop claw size					0.146	0.1050	290.8	-0.7	0.1042
Intercept model							290.8	-0.7	0.0998
<i>Tegula funebris</i> - handling time (generalized linear model)									
Add attempt	-4.11E-06	4.02E-05	6.31E-05	2.71E-05	-6.68E-05	3.82E-05	849	-2	0.9188
Reference			6.30E-05	2.68E-05	-6.71E-05	3.76E-05	847	0	NA
Drop claw size					-7.98E-05	4.01E-05	850.3	-3.3	0.0125
Drop prey size			7.11E-05	2.79E-05			847.9	-0.9	0.06722
Intercept model							851.9	-4.9	0.004761
<i>Nucella ostrina</i> - handling time (generalized linear model)									
Add attempt	0.02172	0.02136	-0.14577	0.02117	0.16318	0.03569	133	-0.9	0.5387
Reference			-0.14536	0.02117	0.16308	0.0357	132.1	0	NA
Drop claw size					0.1549	0.04571	167.8	-35.7	6.56E-12
Drop prey size			-0.1421	0.0239			149.1	-17	4.93E-06
Intercept model							176.7	-44.6	4.66E-15

Table 2.2. Repair frequencies from three localities on the west coast of Vancouver Island (British Columbia, Canada). Both types of repair frequencies are greater for *T. funebris* than for *N. ostrina* at all localities. Wave velocity is in m/s, and N indicates the number of individual gastropods surveyed.

Locality	Wave Velocity	Species	N	%R	RR
Dixon Isl.	1.70	<i>Tegula funebris</i>	200	41%	0.53
		<i>Nucella ostrina</i>	50	22%	0.24
Scott's Bay	1.85	<i>Tegula funebris</i>	230	64%	1.03
		<i>Nucella ostrina</i>	380	45%	0.59
Brady's Beach	5.00	<i>Tegula funebris</i>	100	57%	0.72
		<i>Nucella ostrina</i>	75	49%	0.69

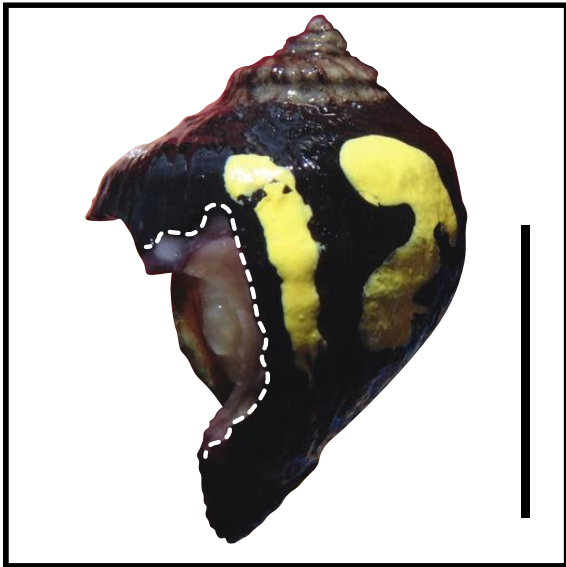


Figure 2.1 Specimen of *N. ostrina* which was attacked in a trial but survived and is in the process of repairing its shell resulting in a repair scar which is outlined in white. The scale bar represents 1cm.



Figure 2.2. *C. productus* attempting to peel a *T. funebris*.

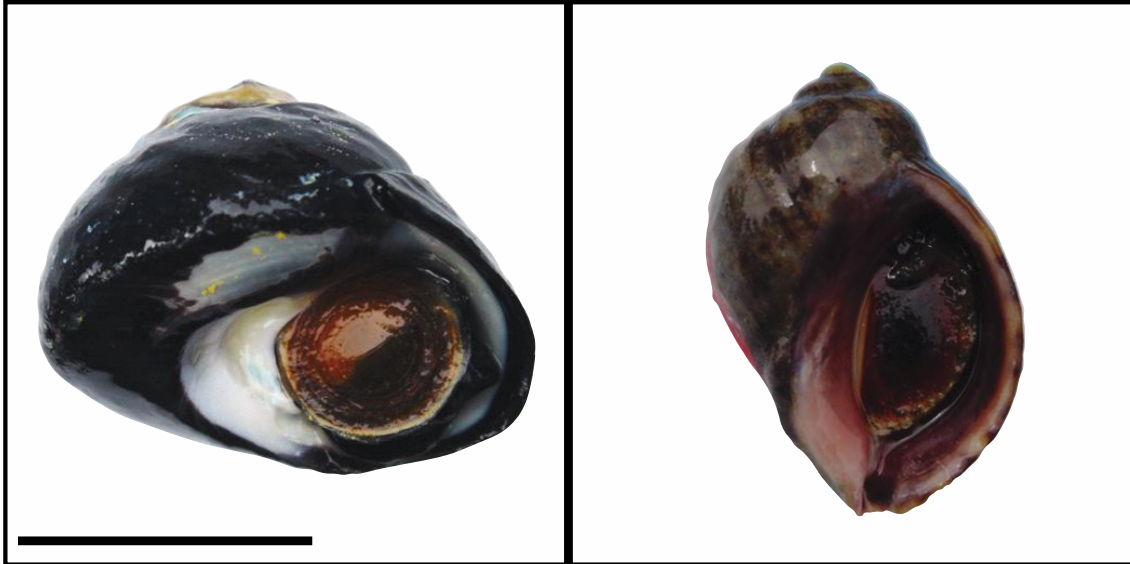


Figure 2.3. Specimens of *T. funebris* (left) and *N. ostrina* (right). Photos are presented at the same scale and the scale bar represents 1 cm.



Figure 2.4. Photo of experimental set up during daytime. Trials were performed at night under red light with the addition of an opaque screen over most of the tank to reduce background light and reflection.

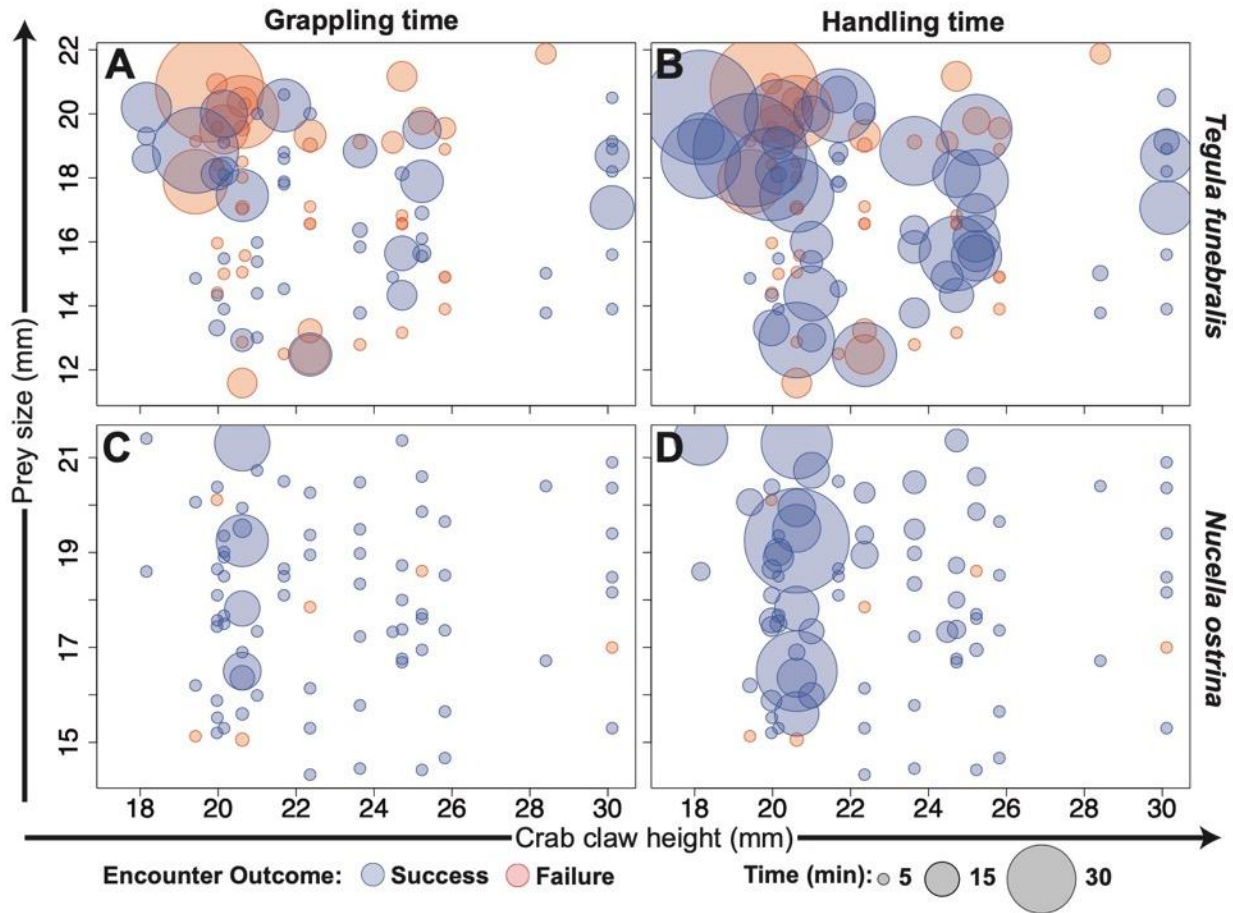


Figure 2.5 Encounter outcomes using point size to indicate the handling or grappling time in the encounter plotted according to prey and predator size (y and x axis respectively) and point color indicating whether encounters resulted in success (blue) or failure (red). A minimum point size of five minutes was used for legibility. The same scale was used for each species of snail. (a) width of *T. funebris* vs. crab chelae height with point size proportional to grappling time, (b) width of *T. funebris* plotted against chelae height with point size proportional to handling time, (c) height of *N. ostrina* plotted against chelae height with point size proportional to grappling time, (d) height of *N. ostrina* plotted against chelae height with point size proportional to handling time.

Conclusion

Repair scars provide an opportunity to study predation when it is difficult or impossible to observe predation events themselves. This study has expanded the current understanding of repair scars by answering questions that concern taxa that are commonly used in repair scars studies. Specifically, the accuracy of repair frequencies measured from single-valve samples and how predator-prey interactions result in repair scars in a model modern system. Including the main goals of this study, there are several important conclusions to this research:

1. Regardless of which valve is used, single valve repair frequencies showed the same trends as did articulated repair frequencies. This finding facilitates the use single-valves in repair scars studies. For disarticulated samples, the most accurate single valve repair frequencies are measured by using the valve presenting the greater repair frequency.
2. Valve affinity does vary between brachiopod taxa and may be dependent on morphology with less more planer concavo-convex brachiopods tending to have dorsal valve affinity. This is a possible avenue of future research. However, single valve samples still showed the same trends in as articulated repair frequencies and despite variation in valve affinity. As well, there was no trend in valve affinity though time and thus, single-valve repair rates are not biased by time.
3. Predator size had an effect on the outcome of crab-gastropod encounters with larger predators being more likely to be successful in Prey species also had a great effect on the outcome with *N. ostrina* being more likely to be killed than *T. funebris* in crab-gastropod encounters.
4. *N. ostrina* had lower repair frequencies than *T. funebris* in natural settings. The results of this study suggest that difference in predator success rate drive this trend with scars

being less likely to result from *N. ostrina* crab-gastropod encounters because of the higher likelihood of prey mortality.

5. Handling and grappling time increased with increasing prey size and decreasing predator size and also was shorter in *N. ostrina* encounters than *T. funebris* encounters. In a natural setting, handling and grappling time may play a role in the outcome of encounters as larger durations would provide bigger windows for interruption of an encounter by predators, competitors, or physical factors such as wave energy. In this instance, prey size, which affected duration of encounters but not the outcome, could have an indirect effect on the outcomes of encounters. The relationship between encounter duration and intrinsic factors realized by this study facilitates future research in determining the effect of external influences on the outcome of crab-gastropod encounters.

In summary, the main objectives of this thesis were to 1) determine how repair frequencies vary between articulated and disarticulated brachiopod samples in the fossil record and 2) determine how predator size, prey size, and prey species affect the generation of repair scars in crab-gastropod encounters. It was found that 1) single-valve repair frequencies closely tracked true, articulated repair frequencies in brachiopod samples and 2) larger predators are more likely to be successful in crab-gastropod encounters but predator success can vary greatly between two species of prey even when the prey are of similar size.

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