Measuring and Interpreting Predation on Gastropod Shells

by

Emily Sue Stafford

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Department of Earth and Atmospheric Sciences
University of Alberta

ABSTRACT

This dissertation focuses on problems and progress in studying crushing predation on gastropods in the Modern and the fossil record. Although crushing predation tends to be destructive, it is possible to gather data on crushing predation from multiple angles. Chapter 2 applies an ichnotaxonomic name, *Caedichnus*, to the trace created by peeling crab predators. Chapter 3 the relationship between shell repair frequency and predation mortality in a modern gastropod community. In this case, repair frequency was likely a direct product of variation in predator abundance and strength. Chapter 4 focused on hermit crabs, an organism that inhabits gastropod shells and exposes those shells to predation even after the original gastropod inhabitant has died. The predatory crabs showed no preference for snail or hermit crab prey, which may mean that hermit crab habitation does not significantly alter the crab-on-snail predation patterns present in a shell assemblage. Chapter 5 expanded on previous work by the author, using a method by G.J. Vermeij to estimate crushing predation in a gastropod assemblage even when individual instances of predatory damage cannot be identified. Vermeij Crushing Analysis (VCA) uses drilled shells to establish a baseline of taphonomic damage in a shell assemblage; the chapter refines and examines this method more deeply, in addition to applying the method to compare predation on modern and fossil gastropod shell assemblages. Chapter 6 is the culmination of the previous chapters, combining predatory traces, VCA, and repair frequency, as well as predatory shell drilling, to examine predation at multiple trophic levels in a Miocene-age fossil shell assemblage from Maryland.

PREFACE

Several chapters of this thesis feature collaborative research involving myself and other researchers. The idea for chapter 2 was conceived by coauthor Murray K. Gingras (University of Alberta), and coauthor Gregory P. Dietl (Paleontological Research Institute) provided the photographed specimens and directive guidance. Lindsey R. Leighton (University of Alberta) gave intellectual and practical feedback on the project. Chapter 2 is now in review as "*Caedichnus*, a new ichnogenus representing predatory attack on the gastropod shell aperture" by E.S. Stafford, G.P. Dietl, M.K. Gingras, and L.R. Leighton, for *Ichnos*.

The ideas and field work behind chapter 3 were a group effort by L.R. Leighton, Carrie L. Tyler (Colorado College), and myself. Chapter 3 is in press as "Gastropod Shell Repair Tracks Predator Abundance" by E.S. Stafford, C.L. Tyler, and L.R. Leighton in *Marine Ecology*, pre-published online.

Chapter 4 is my original work. Chapter 5 is my work, under the guidance of L.R. Leighton, and is in review as "A fossil application of Vermeij Crushing Analysis and comparisons with modern gastropod assemblages from the Pacific Northwest of North America" by E.S. Stafford and L.R. Leighton, for *Palaeogeography, Palaeoclimatology Palaeoecology*.

Chapter 6 is my work, under the guidance of L.R. Leighton, and has been reviewed as "Drilling, durophagy, and a test for trophic cascades in the Miocene St. Mary's Formation" by E.S. Stafford and L.R. Leighton.

DEDICATION

I dedicate this work to my fellow Staffords:
Lisa, Sam, Ruth, and Sue, who encourage and inspire me to do what I want to do.

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CHAPTER 1: INTRODUCTION

Members of the Class Gastropoda inhabit almost every environment available on earth. Gastropods are major constituents of most marine communities and fill numerous ecological roles (examples in Vermeij, 1982; Ray and Stoner, 1995; Behrens Yamada and Boulding, 1998; Rochette and Dill, 2005). One key to gastropod success is the hard shell that most possess. A predator must pry the shell open, drill into it, chip or crush it, or otherwise bypass the shell to consume the flesh. The advent of durophagous predators likely spurred shell evolution in many gastropod lineages (Vermeij, 1977, 1987).

Durophagous predation on gastropods has a deep history. Paleozoic durophages included mollusks and arthropods, but the Mesozoic Era saw the appearance of what are now the most abundant and diverse groups of crushing predators: the brachyuran crabs, stomatopod crustaceans, teleost fishes, and rays (Walker and Brett, 2002). Naticid and muricid gastropods, major predatory drillers, also appeared in the Mesozoic. This flourishing of predatory groups has been termed the Mesozoic Marine Revolution (MMR) (Vermeij, 1977), and was in fact a series of radiations that continued into the Cenozoic (Walker and Brett, 2002).

Possibly in response to the increasing abundance and ability of durophages, particularly brachyuran crabs, the defensive potential of gastropod shells also increased, especially in the Late Mesozoic and into the Cenozoic (Vermeij, 1977, 1987). Thicker shells can reduce predator success, and certain gastropods develop thicker shells in the presence of chemicals from predators or injured conspecifics (Appleton and Palmer, 1988; Trussel, 2000; Bourdeau, 2009).

Durophagous brachyuran crabs employ two general methods of attack: the outright crush and a chipping/peeling method (Zipser and Vermeij, 1978). The peeling method leaves the empty shell with a signature, V-shaped break in the aperture. This type of damage has been observed in modern laboratory settings (Bertness and Cunningham, 1981; West et al., 1991; Donovan et al., 1999) and has been documented in the fossil record (e.g., Vermeij et al., 1980; Allmon et al., 1990). However, the shell damage caused by the outright crush, and “messier” instances of peeling, can be confused with taphonomic damage.

To understand the influence of crushing predation on gastropod evolution and in modern ecological communities, it is necessary to quantify predation and its effects. Crushing predation, in particular, can be difficult to quantify because it is essentially destructive: the most fossilizable component of the prey organism is damaged, reducing preservation potential.

There are two primary ways to quantify crushing predation: repair scars (traces of failed crushing attacks) and unrepaired traces. With repair scars, the gastropod survived a predatory attack and repaired its damaged shell. Repairs are useful because they are easy to identify and count; however, the interpretation of repair scars is ambiguous, as variation in repair frequency can reflect changes in attack frequency or changes in attack success, with differing consequences for predation mortality (Leighton, 2002; Alexander and Dietl, 2003). Chapter 3 addresses the relationship between repair frequency and mortality in a modern community.

Traces of successful predation have an advantage over repair scars in that they are directly related to mortality. Some instances of crushing predation, peeling predation, can leave distinct, identifiable traces on the victims' shells. Chapter 2 addresses these traces from an ichnological perspective.

Information about predation may also be gleaned from fragmented shells, even if individual peeling traces are not identifiable. Chapter 5 builds upon Stafford and Leighton (2011), refining Vermeij's (1982) method of estimating crushing frequency by controlling for taphonomic damage. Chapter 5 addresses issues of methodology and interpretation, and also applies Vermeij Crushing Analysis to a fossil gastropod assemblage for comparison with modern assemblages. Chapter 6 integrates Vermeij Crushing Analysis and repair frequency to examine predation at multiple trophic levels in a fossil gastropod assemblage.

A problem with the quantification of predation on gastropods is hermit crab habitation. Hermit crabs utilize gastropod shells as domiciles, exposing the shells to many of the same predators gastropods encounter (Walker, 1989). It is not clear whether predation on hermit crabs distorts predation patterns from the original gastropod assemblage. Chapter 4 examines the predatory behavior of a durophagous crab on both gastropod and hermit crab prey.

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CHAPTER 2

CAEDICHNUS, A NEW ICHNOGENUS REPRESENTING PREDATORY ATTACK ON THE GASTROPOD SHELL APERTURE, AND A REVIEW OF SHELL-BREAKING PREDATION ON GASTROPODS[1]

INTRODUCTION

Trace fossils record the behaviors of organisms in a variety of substrata. Typically, these traces are found in rock, representing the activities of organisms in the sediment before lithification (Frey and Seilacher, 1980); however, trace fossils also occur on fossilized skeletal material, representing the varied activities of tracemaking organisms upon other organisms (e.g., Bromley, 1981; Brett, 1985; Bromley and D'Alessandro, 1990; Tavernier et al., 1992; Hagan et al., 1998; Nielsen and Nielsen, 2001; Wilson and Palmer, 2006; Ishikawa and Kase, 2007; Jagt, 2007; Walker, 2007).

Durophagous predation, wherein predators crush or otherwise damage hard shells to access the prey within, is an instance in which trace fossils occurring on body fossils are informative of biotic interactions. Paleoecologists and ecologists use the occurrence of predation traces, such as drillholes and crushing repair scars, to examine not only mortality patterns in gastropod populations, but also patterns of prey preference and attack technique among the predator population(s), as well as evolutionary trends among prey lineages (e.g., Vermeij et al., 1981; Allmon et al., 1990; Kelley, 1991; Hansen and Kelley, 1995; Kelley and Hansen, 1996; Cadée et al., 1997; Dietl and Alexander, 2000; Kowalewski et al., 2000; Alexander and Dietl, 2001; Złotnik, 2001; Złotnik and Ceranka, 2001; Harries and Schopf, 2003; Grey et al., 2006; Donovan and Harper, 2007; Simões et al., 2007; Skovsted et al., 2007; Dietl and Alexander, 2009; Nagel-Myers et al., 2009; Leighton et al., 2013).

Herein, we assign the new ichnogenus *Caedichnus* to the predatory trace on gastropod shells resulting from an attack on the shell aperture (Fig. 2-1). The trace has been identified and studied in detail by many workers (e.g., Ebling et al., 1964; Muntz et al., 1965; Shoup, 1968; Rossi and Parisi, 1973; Heller, 1976; Vermeij, 1976; Zipser and Vermeij, 1978; Elner and Raffaelli, 1980; Bertness and Cunningham, 1981; Bertness, 1982; McLean, 1983; du Preez, 1984; Chilton and Bull, 1986; Thomas and Himmelman, 1988; West et al., 1991; Seed and

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[1] A version of this chapter has been submitted for publication. Stafford et al., *Ichnos*

Hughes, 1995; Yamada and Boulding, 1997; Quensen and Woodruff, 1997; Dietl and Alexander, 1998). The trace has yet to be formally described as an ichnofossil. There is precedent for the ichnotaxonomic description of predation traces, for example the ichnogenera *Oichnus* (Bromley, 1981) (holes bored by predatory gastropods; perhaps synonymous with *Sedilichnus* (Müller, 1977) and *Tremichnus* (Brett, 1985)) and *Belichnus* (Pether, 1995) (holes punctured by predatory stomatopods) (see Bromley, 2004 for a partial review of marine bioerosion). Like *Oichnus* and *Belichnus*, *Caedichnus* is informative of both the predatory conditions that prey endured and also the predatory behavior and feeding preferences of the attackers.

Considering the cosmopolitan distribution and long geologic history of both gastropods and crushing predators, the identification of this trace is valuable in understanding the ecology and evolution of these organisms through time. An ichnotaxonomic description of these traces will provide a universal term for researchers to apply when identifying and examining such predation traces.

Crushing Predation on Gastropod Shells

Gastropods encounter crushing predators in marine and many freshwater and terrestrial environments (e.g., Zipser and Vermeij, 1978; West et al., 1991; Cadée, 1994). Specialized methods of breaking gastropod shells tend to leave stereotyped damage on the prey's shell; that is, the damage is identifiable in its consistent appearance and location on the prey shell. The confidence with which such damage can be attributed to predation, or even to a particular predator, depends on several factors. Especially important are the size and architecture of the prey shell and the size and feeding apparatus of the predator, which combine to determine the predator's method of attack and likelihood of success.

The shell aperture, as the only point of entry in most gastropod shells, is inherently vulnerable. Predators may access prey tissues by chipping, smashing, or peeling the aperture lip to expose the animal within. In evolutionary response, many gastropod lineages defend themselves with narrowed apertures, thickened aperture lips, or occlusive teeth that obstruct the aperture (Vermeij, 1987).

A gastropod that survives an attack can repair its damaged shell, leaving a noticeable scar. Repair scars are usually visible as disruptions in the growth lines, surface ornament, or color pattern of the shell (Fig. 2-2). The geological history of shell repair on large, shelled animals extends at least to the Cambrian (Ebbestad and Peel, 1997, and references therein; Alexander and Dietl, 2003, and references therein; Leighton, 2011, and references therein), but the earliest-known gastropod shell repairs (and thus the earliest evidence of aperture-attack predation) date from the Ordovician (Steele and Sinclair, 1971; Rohr, 1993; Horny and Peel, 1996; Horny, 1997; Alexander and Dietl, 2003; Lindström and Peel, 2005; Ebbestad and Scott, 2007). Repair scars are not only present, but sometimes common among Ordovician gastropods and gastropod-like mollusks (Ebbestad and Peel, 1997; Ebbestad et al., 2009; Lindström and Peel, 2005), and are identical to those observed on modern gastropods. Gastropod repair scars occur consistently through to the present (Vermeij, 1987; Alexander and Dietl, 2003).

In the Paleozoic record of shell repair, many types of arthropods and vertebrates have been implicated due to potential durophagous feeding specializations such as grinding jaws (Vermeij, 1987; Brett and Walker, 2002; Alexander and Dietl, 2003; Leighton, 2003). For the peeling scars seen on Paleozoic gastropods, smaller arthropods are among the likely culprits (Schram, 1981; Rolfe and Dzik, 2006; Kühl et al., 2009). After the Paleozoic, more familiar groups of crushing predators emerged, particularly the crustaceans that are responsible for much of the aperture damage observed in modern systems (Walker and Brett, 2002).

Crushing Damage to Gastropod Shells

The nature of predatory damage on gastropod shells depends on the crushing apparatus of the predator, the shell defense traits of the prey, and the size of the predator relative to the prey. Irrespective of the identity of the predator, we can group gastropod shell-crushing damage into six general categories: complete fragmentation (Fig. 2-3.1); spire damage (Fig. 2-3.2); columella damage (Fig. 2-3.2); holes in the body whorl (Fig. 2-3.3); and lastly, aperture damage, which comprises a continuum from minor chipping (Fig. 2-3.4) to aperture peeling (Fig. 2-3.5). Although the focus of this paper is aperture damage, it is useful to review these other types of damage (Table 2-1), both to distinguish what types of damage fall within *Caedichnus* and as a reminder that predatory tracemakers can produce multiple types of damage in a single attack.

Complete fragmentation (Fig. 2-2.1) suggests a powerful predator that is large relative to the prey. It may result from outright crushing by a decapod crustacean, smashing by a relatively large stomatopod crustacean (e.g., Full et al., 1989; Patek and Caldwell, 2005), grinding in the jaws of a teleost fish or ray (e.g., Garrity et al. 1985; Slootweg, 1987; Lundeba et al., 2011) or in the gizzard of a bird (e.g., Cadée, 1994, 1995), or crushing in the jaws of a reptile or mammal (e.g., Dalrymple, 1979; Spivey, 1993; Tucker et al., 1997; Bennett, 2002; Dehn et al., 2007) (Table 2). This category of damage may be difficult to distinguish from taphonomic (post-mortem, non-predatory) damage (although distinguishing is not impossible (Oji et al., 2003; Kosloski, 2011; Salamon et al., 2014)).

Spire damage (Fig. 2-2.2) and columella damage (Fig. 2-2.3) and body whorl damage (Fig. 2-2.4) are caused by more focused forces, when predators apply their chelae (claws) or mouthparts to these respective regions of the shell. Because predators may try several methods of attack on shells that are too large or strong to crush outright, these types of damage often co-occur on gastropod shells.

Aperture chipping (Fig. 2-3.4), akin to "scalloped" damage *sensu* Alexander and Dietl (2003), can occur due to a weak attack by a decapod, or as incidental damage from passing through the jaws or gizzard of a vertebrate predator. Aperture chipping can also result from gastropod behaviors. Busyconine whelks use their aperture lip to wedge open bivalve prey, often incurring minor damage to their own aperture (Dietl, 2003; Dietl et al., 2010). Even particularly extreme wedging scars typically can be distinguished from crab peels (Dietl, 2003).

Aperture peeling (Figs. 3.5, 4, 5) is caused almost exclusively by crustacean predators. In Alexander and Dietl's (2003) review of predatory repair scars, such damage was described as "embayed breakage". Material is removed from the shell whorls, starting at the outer lip of the aperture. The predator continues until it can access the withdrawn prey (gastropod or hermit crab); depending on how deep the prey can withdraw, the peel may reach further up the spire, exposing several whorls. Highly specialized predators tend to peel more deeply than less-specialized predators (see Known Crustacean Predators). The severity of the peel can be described by its aspect ratio: height of the damaged portion at the apertural lip divided by the depth of the damage into the whorl (measured around the shell whorl(s)) (Fig. 2-6).

The high degree of specialization required to peel the aperture of a gastropod shell means that aperture peeling is a strong indicator of predation. Peel-like damage is unlikely to be attributable to taphonomic factors (Stafford and Leighton, 2011), whereas other types of damage may be less-certainly ascribed to predation. Aperture damage frequently occurs in both unrepaired and repaired states, allowing assessment of the relative efficiencies of predator attacks and prey defenses. The very fact that this type of damage is frequently repaired speaks to the importance of aperture attacks in the evolution of gastropods. It is only through differential survival that predation can drive changes in the defensive morphologies and behaviors of prey species (Vermeij, 1987). The presence of repaired aperture damage in fossil and modern gastropods records a history of the selective influence of peeling predation.

PREDATORY ORIGIN OF THE TRACE

Caedichnus represents predation by crustaceans, or other aperture-attacking predators, on gastropod shells (see Table 2-2). The value of this trace as a positive indicator of predation demands that it can be distinguished from taphonomic (post-mortem) shell damage. Crashing waves or boulders tend to fragment shells catastrophically (Zuschin and Stanton, 2001; Zuschin et al., 2003). Repetitive wave action gradually abrades shells, creating smooth edges and stripping surface material (Oji et al., 2003; Salamon et al., 2014); abrasive damage to the aperture is associated with overall polishing of the shell (Ogaya, 2004). Exposure to shell-weakening boring organisms or chemical conditions can increase the likelihood of abiotic shell facture, but this damage is unlikely to be confused with predatory damage (Rodrigues et al. 2008). Peel-like taphonomic damage has been reported (Schäfer, 1962, referred to in Zuschin et al., 2003), but is otherwise absent in the literature. Kosloski (2011) found that microstructural deformation observed on the breakage surfaces of the shells reflect the contrasting effects of shearing (crab predation) versus tensile stress (point-loading) (Kosloski, 2011). Thus, predatory damage on shells is distinguishable from taphonomic damage on multiple scales.

IDENTIFYING PREDATORS AND PREY

Caedichnus occurs on gastropod shells, but the presence of the unrepaired trace does not necessarily indicate predation upon the original gastropod inhabitant. The predators that peel the shells of live gastropods may similarly attack shells housing hermit crabs (Shoup, 1968; Rossi and Parisi, 1973; Bertness and Cunningham, 1981; Bertness, 1982; McLean, 1983; Weissberger, 1995). Crabs have even been known to attack empty shells (Walker and Behrens Yamada, 1993), but the prevalence and impact of this behavior requires further study.

Rossi and Parisi (1973) observe slight, but inconsistent, preferences for hermit crab prey by crab predators; other workers have found that durophages tend to attack shells indiscriminately (see LaBarbera and Merz, 1992). Hermit-crab-inhabited shells tend to be structurally weaker, thus potentially more vulnerable, than those of live gastropods (LaBarbera and Merz, 1992). Furthermore, hermit crabs can cause shells to be transported from their original habitats into new ones (Walker, 1989), so one cannot assume that the hermit crabs endured the same predatory conditions as the gastropods that originally secreted the shells.

Hermit crab habitation of gastropod shells is often indicated by the presence of particular types of damage associated with hermit crab use, as well as with the boring and encrusting organisms that colonize hermit-crab-inhabited shells (Walker, 1992). Hermit crabs drag their shells, abrading the surface on the substratum, and can leave fine marks where their legs gripped the inside of the shell (Walker, 1989). A shell may remain in a hermit crab population for many generations, until it becomes too damaged to use or is otherwise removed. Over time, shells can accumulate extensive borings, particularly around the aperture or within the shell (Walker, 1989). Certain borings, such as the trace *Helicotaphrichnus commensalis* (Kern et al., 1974) (a spionid domicile boring) are strictly associated with hermit crabs (Kern et al., 1974). Extensive borings on the shell of an infaunal gastropod, even if they are not strictly associated with hermit crabs, indicate that shell was likely exposed to hermit crabs after the death of the gastropod. Note that some borers and encrusters do occur with living gastropods (e.g., Stefaniak et al., 2005), so the presence of borings (with the exception of hermit-crab-specific traces) is not necessarily an absolute indicator of hermit crab habitation.

If a hermit crab at some point inhabited a shell after the death of the gastropod (see Walker, 1992), it may be possible to determine whether a peeling trace was created before or after the hermit-crab-associated damage. Ishikawa et al. (2004) noted, for example, that multiple *H. commensalis* borings on a single shell suggest a scenario in which a hermit-crab-inhabited shell, already possessing a spionid commensal, is peeled, creating a new aperture for a subsequent spionid worm to excavate. Ishikawa et al. (2004) used such hermit-crab-specific traces in their “endobiont” method of estimating the degree to which peeling in a shell assemblage is due to predation on hermit crabs, rather than on gastropods. Repaired peels, a frequently used measure of predation in the fossil record (Alexander and Dietl, 2003), clearly indicates an attack on a gastropod, as hermit crabs are incapable of repairing the shell.

Identification of the predator responsible for *Caedichnus* is more ambiguous than identifying the prey organism, because predators are generally not caught with their claws or jaws in the proverbial cookie jar, especially in the fossil record. There are numerous extant predators, particularly crustaceans, known to peel gastropod shells. The morphology of the peel offers clues to the size, strength, and even identity of the predator.

Known Crustacean Tracemakers

The most notable shell-peeling predators come from the crustacean Order Decapoda, including the infraorders Brachyura (true crabs), Anomura (including hermit crabs), Achelata (including spiny lobsters), and Astacidea (including true lobsters) (Schweitzer and Feldmann, 2010). By far, the best-studied durophages are the brachyuran crabs. The earliest known brachyuran crabs are Jurassic in age (Schweitzer and Feldmann, 2010), though many of the important durophagous superfamilies did not arise until later (Alexander and Dietl, 2003; Schweitzer and Feldmann, 2010).

Most crustaceans use peeling (or aperture chipping) when the prey is too large, or its shell too thick, to be crushed outright (Zipser and Vermeij, 1978; West et al., 1991). The predator uses chelae or mandibles to break successively deeper chips in the gastropod shells' apertural margin until the flesh is exposed (Shoup, 1968; Shigemiya, 2003; Ogaya, 2004). The depth of the peel depends in part on how deeply the prey can retract into its shell and on the degree of specialization and peeling technique of the predator (Rossi and Parisi, 1973; Hughes and Elner, 1979; Lawton and Hughes, 1985; Allmon et al., 1990).

"Xanthoid" crabs (a diverse group including families within the superfamilies Xanthoidea, Eriphioidea, and Carpilioidea, which were previously included in Xanthoidea) and box crabs (family Calappidae) are typical among crushing crabs in that they have very large, heteromorphic chelae with large, blunt, crushing molars (Schweitzer and Feldmann, 2010). Calappids and some "xanthoids" use a prominent tooth on the major chela like a can-opener (Shoup, 1968; Seed and Hughes, 1995; Ogaya, 2004; Dietl and Vega, 2008). Calappid peels tend to be deeper than those of other predators (Rossi and Parisi, 1973). Calappids and stone crabs (*Menippe mercenaria*) have also been observed to puncture holes in the body whorl of the shell during the peeling process (Savazzi, 1991; Dietl et al., 2010). "Xanthoids" and calappids are particularly abundant in tropical regions, and their powerful claws allow them to process large prey relative to their body size (Vermeij, 1977).

Temperate crabs tend to be less specialized for crushing predation. The rock crabs (superfamily Cancroidea) do not have strongly heteromorphic chelae (Seed and Hughes, 1995), but are sufficiently strong to crush and peel gastropod shells. Swimming crabs (superfamily Portunoidea) compensate for their lack of power with versatility, using the slender, heteromorphic "crusher" and "cutter" claws to peel gastropod shells (Elner and Raffaelli, 1980). The small crabs of the superfamily Grapsoidea are not well adapted for hard prey, but do feed opportunistically on small gastropods (Woodruff, 1978; Yamada and Boulding, 1996; Quensen and Woodruff, 1997).

Spiny lobsters and slipper lobsters (infraorder Achelata) lack chelae, and thus peel shells using their mandibles (Kent, 1979; McLean, 1983; Lau, 1987; Takahashi et al., 1995). The laterally asymmetrical mandibles function similarly to the calappid crusher chela, and produce a similar peel (Randall, 1964; Vermeij, 1978; Iversen et al., 1986).

Lobsters and crayfish (infraorder Astacidea), have large chelae. Lobsters typically use their larger chela to peel or chip the aperture of large gastropods (Thomas and Himmelman, 1988), but have also been observed peeling with their mouthparts, similar to spiny lobsters (Weissberger, 1995). Crayfish, despite their enlarged chelae, peel using their mouthparts (Alexander and Covich, 1991; Brown, 1998; Nyström and Pérez, 1998; DeWitt et al., 2000).

Hermit crabs (infraorder Anomura), are usually considered generalist feeders and only opportunistic molluscivores, but the giant hermit crab *Petrochirus diogenes* may chip the aperture of *Strombus gigas* to reach the flesh (Iversen et al., 1986) and *Pagurus hirsutiusculus* can peel the *Littorina scutulata* shells borne by small *Pagurus granosimanus* (pers. obs.).

Mantis shrimp (Family Gonodactylidae, Order Stomatopoda), better known for punching holes into or shattering prey shells using a specialized, club-like dactyl (Pether, 1995; Patek and Caldwell, 2005), can use the dactyl to chip away the shell aperture until the prey is exposed, creating a very deep peel (Bertness, 1982) akin to that of a calappid crab.

Known Vertebrate Tracemakers

Vertebrate molluscivores are usually much larger than their prey, and thus crush gastropod shells outright using jaws or gizzards, resulting in total fragmentation (Table 2-1). An unusual case is rats (*Rattus* spp.), which bite through the shell from the aperture, working around the spiral until they reach and sever the columellar muscle (Joshi et al., 2006), leaving a trace similar to that produced by peeling crustaceans (Parisi and Gandolfi, 1974; Navarette and Castilla, 1993; Moreno-Rueda, 2009). Rats may leave the (often thickened) apertural lip intact, peeling only through the thinner shell of the body whorl (Parisi and Gandolfi, 1974; Quensen and Woodruff, 1997; Moreno-Rueda, 2009). The distribution of peeling traces in rat middens suggests that peeling is a learned or discovered, rather than instinctual, behavior (Navarette and Castilla, 1993). Rats' gastropod prey can be terrestrial, freshwater, or intertidal, but the empty damaged shells are found exclusively on land (Navarette and Castilla, 1993).

Hydrobia, which were swallowed whole then passed through the gizzards of molluscivorous shelducks, exhibited both lethal and nonlethal aperture damage; i.e., some damaged gastropods were expelled alive (Cadée, 2011). This is an atypical case of peel-like damage being produced by a non-peeling predator.

ECOLOGICAL INTERPRETATION OF THE TRACE

The occurrence of *Caedichnus* can suggest the frequency of predatory peeling in a system, but is unlikely to be an exact estimate of the overall frequency of crushing predation. Large crushing predators (e.g., crushing fish) may destroy their prey's shells (Table 2-2). Even among known peeling predators, peeling behavior is mediated by relative prey size and morphology, and may not be the only predatory behavior (e.g., Hughes and Elner, 1979; Lawton and Hughes, 1985; Schindler et al., 1994; Ray-Culp et al., 1999; Cote et al., 2001; Harding, 2003). The frequency of *Caedichnus* in an assemblage likely underestimates total durophagous behavior in most systems.

Although *Caedichnus* is not a proxy for overall durophagy, it represents an important ecological interaction between predators and prey. The predators are powerful enough to attack the prey, but still weak enough that they must manipulate and slowly break the shell, rather than crush it outright (Hughes and Elner, 1979; Lawton and Hughes, 1985; Schindler et al., 1994; Behrens Yamada and Boulding, 1998). The extended handling time and energy expenditure of peeling increases the chance that the predator will drop or abandon the prey, leading to repair scars (Schindler et al., 1994). As noted by Vermeij (1987), a repair indicates a predator-prey encounter in which the prey survived. If potentially anti-predatory shell traits (e.g., thickness, aperture shape, or ornament) increase handling time and reduce predator success, gastropods with these traits, or hermit crabs that choose shells with these traits, have a selective advantage (Vermeij, 1982).

Repaired peels are frequently noted in fossil gastropod assemblages. The identification of unrepaired and repaired peels in fossil and modern shell assemblages permits the exploration of shell repair as a proxy for crushing predation and as an indicator of prey defensive advantage (Vermeij, 1987). The frequency of *Caedichnus* in gastropod shell assemblages, used as a relative estimate of predatory mortality, may indicate the intensity of predation as a selective force on gastropods (and/or hermit crabs). Such knowledge enables researchers to correlate predation pressure with prey morphological evolution and to pinpoint times and places of major predatory escalation.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Caedichnus* n. igen.

***Type ichnospecies*:** *Caedichnus spiralis*, n. isp.

***Diagnosis*:** Excision of gastropod shell material, beginning at outer lip of aperture and extending backwards at least 5° into whorl with an aspect ratio of at least 0.3. Aspect ratio is defined as the depth of damage perpendicular to growth margin divided by height of damage parallel to growth margin. Trace ranges from slivers of shell removed from aperture, subparallel to growth margin and potentially cross-cutting ornament; to larger portions of material removed, resulting in arcuate (V-shaped), W-shaped, or semicircular geometries. Extent of breakage parallel to growth margin is limited only by height of aperture. Extent of breakage perpendicular to growth margin is limited only by extent of shell's whorls. Breakage profile can be jagged or clean. Breakage surface (when fresh and unrepaired) is sharp. In cases of repaired damage, the breakage can be marked by a disruption in shell surface topography. Disruption varies in depth depending on shell thickness, due to new shell growth commencing from interior surface of shell. With repaired damage, shell surface features, such as ornament or color patterns, can exhibit a slight to prominent mismatch between original shell and new growth.

***Etymology*:** From the Latin *caedere*, meaning "to cut or hew" or "to kill". One derivative of *caedere*, *cisus*, is the etymological ancestor of the English word "scissors", imitative of the peeling technique employed by some crustaceans. Another derivative, *cidere*, gives English the "-cide" in "homicide" or "pesticide", alluding to the predatory origin of this excision.

***Occurrence*:** Worldwide; Ordovician to present (Alexander and Dietl, 2003, and references therein).

Remarks**:** *Caedichnus* commonly extends only partway into the body whorl of the shell, but can extend through the complete body whorl or through multiple whorls. This includes minor "scalloped" breaks and deeper "embayed" breaks (*sensu* Alexander and Dietl, 2003). Extensive (multi-whorl) traces are more likely when the predator is highly specialized for peeling, the prey shell has multiple spire whorls, and the prey animal can withdraw deep into the shell.

Caedichnus is defined as aperture breakage extending at least 5° into the whorl with an aspect ratio greater than 0.3, because less severe damage can have non-predatory origins. For example, gastropod shells can be damaged by contact with hard substrates, while the gastropod is alive or post-mortem. Several groups of predatory gastropods use the aperture to wedge open the shells of their bivalve prey (Dietl, 2003; Dietl et al., 2010). Such damage tends to be more extensive parallel to the growth margin than perpendicular to the margin, but even extensive wedging scars can be distinguished from crab peels (Dietl, 2003).

Although predation is a plausible explanation for many instances of less-extensive damage (depth less than 5° or aspect ratio less than 0.3), the other potential causes are not within the definition of the behavior represented by *Caedichnus*. *Caedichnus* is thus limited to unambiguous instances of predatory aperture damage.

Caedichnus can co-occur with other types of predatory damage to gastropod shells, such as removal of the spire or lower portion of the columella, or holes punctured in the body whorl or spire. *Caedichnus* can cut across, or be crosscut by, other trace fossils in instances in which boring or encrusting organisms interacted with the shell before or after the production of the trace.

The earliest records of *Caedichnus* are repaired examples on Ordovician fossil gastropod shells (Steele and Sinclair, 1971; Rohr, 1993; Horny and Peel, 1996; Horny, 1997; Alexander and Dietl, 2003; Lindström and Peel, 2005; Ebbestad and Scott, 2007). It is possible that unrepaired (likely fatal) examples of the trace are present in Ordovician assemblages, but have not been identified as predatory damage.

Caedichnus spiralis n. igen. et n. isp.

Figs. 1, 7, 8

Diagnosis**:** As for ichnogenus, by monotypy.

Material**:** Holotype, fig. 2-1, *Fasciolaria* sp., Lower Waccamaw Formation, early Pleistocene, collected at Holloman Pit, Columbus County near Whiteville, North Carolina (PRI

68130); Paratype, fig. 2-7.1, *Strombus evergladesensis* peeled approximately 450° from the aperture, Bermont Formation, lower Pleistocene, collected at Palm Beach Aggregates, Loxahatchee, FL, USA (PRI 68131); Paratype, fig 2-7.2, *Heilprinia carolinensis,* Lower Waccamaw Formation, early Pleistocene, collected at Prince Farm, Columbus County near Old Dock, North Carolina (PRI 68132); Paratype, fig. 2-8.1, *Strombus evergladesensis* peeled almost 360° from the aperture, Bermont Formation, lower Pleistocene, collected at Palm Beach Aggregates, Loxahatchee, FL, USA (PRI 68133); Paratype, fig. 2-8.2, *Strombus evergladesensis* with repaired peel over 180° deep, Bermont Formation, lower Pleistocene, collected at Palm Beach Aggregates, Loxahatchee, FL, USA (PRI 68134).

Etymology**:** the Latin for “spiraling”, referring to how the trace follows the spiraling whorls of the shell.

Occurrence**:** as for ichnogenus, by monotypy.

Remarks**:** Currently, we are establishing *Caedichnus spiralis* as a monospecific ichnogenus. Examples of the trace vary in extent of peel from the aperture. Although this variation is suggestive of differences in the relative size and power of the predator to prey or the predator’s degree of specialization in peeling gastropod shells, this variation is gradational. Splitting the ichnogenus into ichnospecies based on an arbitrary threshold would unnecessarily and inappropriately restrict the interpretation of the trace. Many different predators may produce similar traces, and a single predator may produce variable traces.

In addition to ichnofossil specimens, incipient *C. spiralis*, unrepaired and repaired, is common on modern gastropod shells. Figures 2-2 and 2-4 show examples, produced by predators in the laboratory and collected in the field, to illustrate variation in the trace.

CONCLUSIONS

We define the ichnogenus *Caedichnus* to describe the wedge-shaped excision of shell material from the outer lip of the aperture of a gastropod shell as a result of peeling predation. This trace can extend through several whorls, depending on the peeling ability of the predator and the depth of withdrawal of the prey. The attack methods used to produce this trace are prone to failure, creating the opportunity for differential survival of prey animals that produce (or inhabit) better-defended shells. The frequency of *Caedichnus* in gastropod shell assemblages may serve as a proxy for the predation pressure endured by both the living gastropod and hermit crab populations.

FIGURES

Figure 2-1. *Caedichnus spiralis* Holotype (PRI 68130): *Fasciolaria* sp., Lower Waccamaw Formation, early Pleistocene, collected at Holloman Pit, Columbus County near Whiteville, North Carolina; peeled almost 360° from aperture. Scale bar = 2 cm. Specimen rotated to show extent of damage.

Figure 2-2. Repaired aperture peeling damage on modern shells (incipient repaired *Caedichnus spiralis*) *1. Fasciolaria tulipa*, collected in Florida. Initial damage extended less than 90° from aperture. Scale bar = 2 cm. *2. Terebra subulata* shell collected at Tilic Bay, Lubang Island, Philippines. Initial damage extended over 360° from aperture. Scale bars = 2 cm. Specimen rotated in the three detail views, to show the extent of damage. The upper right and lower right details also show a second, shallower repaired trace below the 360° scar. Note the distortions in growth lines, spiral ornament, and color in the regrown shell material.

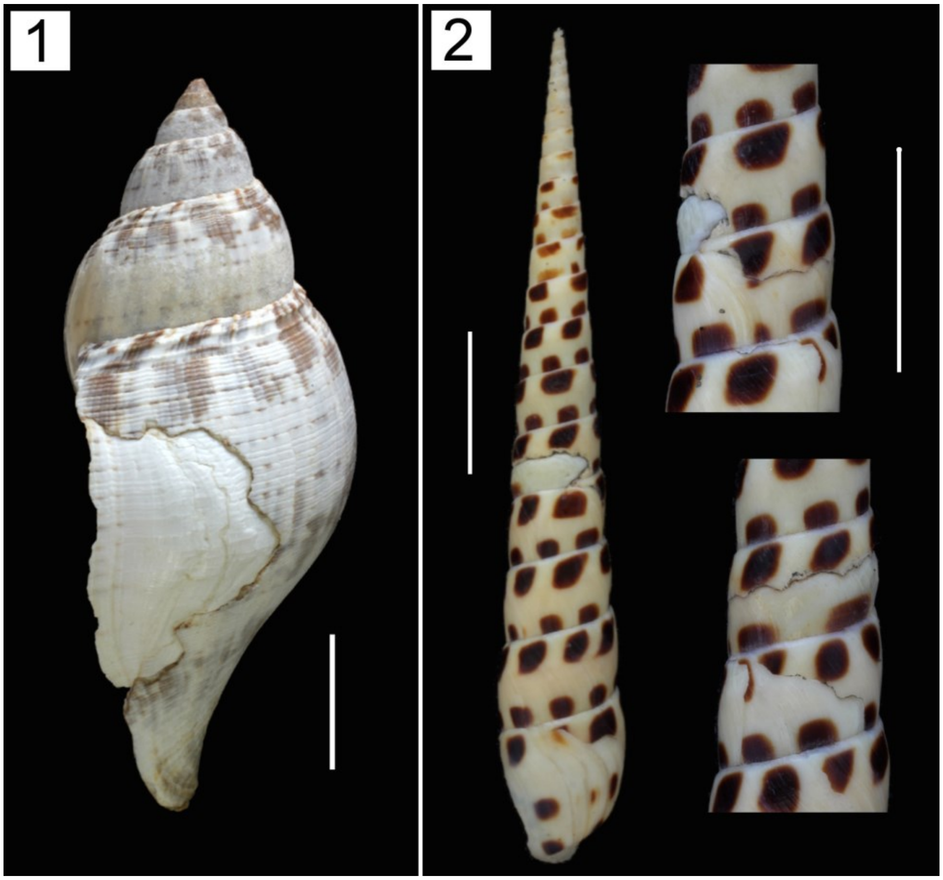

Figure 2-3. The major types of damage that crushing predators (particularly crustaceans) inflict on gastropod shells. *1*. Total fragmentation; *2*. Spire/apex damage and columella/siphonal canal damage; *3*. Hole in body whorl; *4*. Aperture lip chipping; *5*. Aperture peel; *6*. An intact shell for reference.

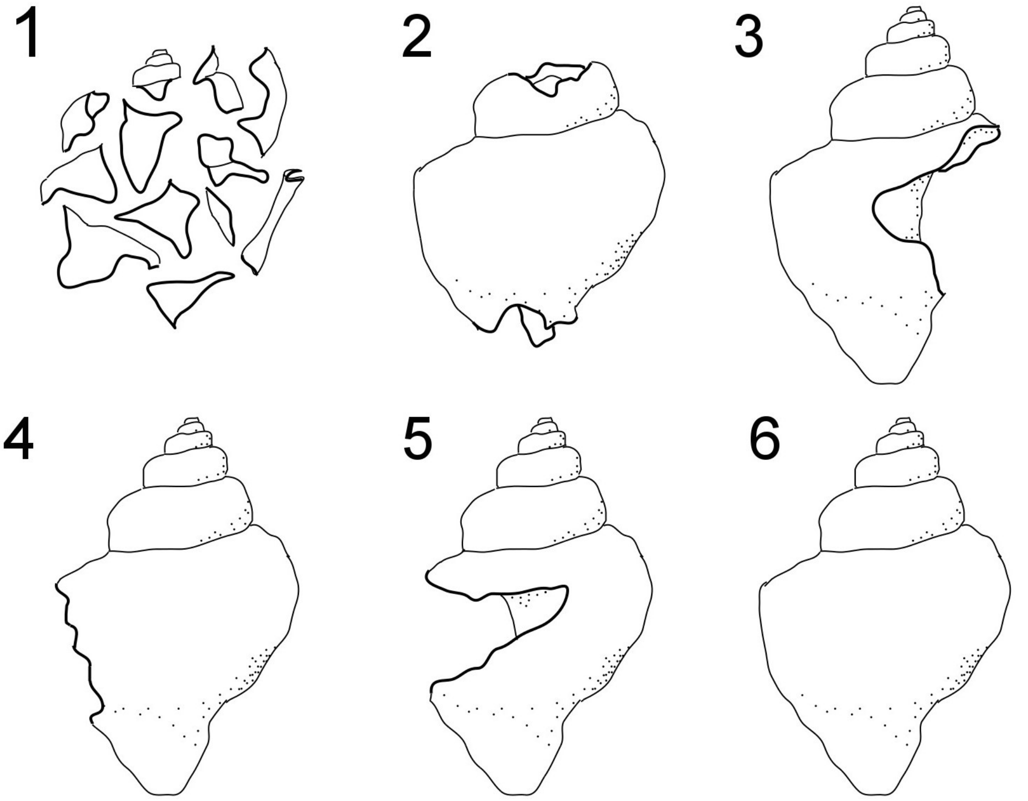

Figure 2-4. Modern examples of aperture peeling damage (incipient *Caedichnus spiralis*). *1. Strombus alatus* shell, damaged by *Menippe mercenaria* in laboratory (Center for Marine Science, University of North Carolina, Wilmington; Wilmington, North Carolina, USA). Trace extends over 90° from the aperture. *2. Busycon carica* shell, damaged by *Menippe mercenaria* in laboratory (Paleontological Research Institution, Ithaca, New York, USA). Trace extends approximately 45° from the aperture. *3. Fasciolaria hunteria* shell, inhabited by a hermit crab, peeled by *Menippe mercenaria* in laboratory (Center for Marine Science, University of North Carolina, Wilmington; Wilmington, North Carolina, USA). Trace extends approximately 450° from the aperture. Scale bars = 2 cm. Specimens rotated to show the extent of damage.

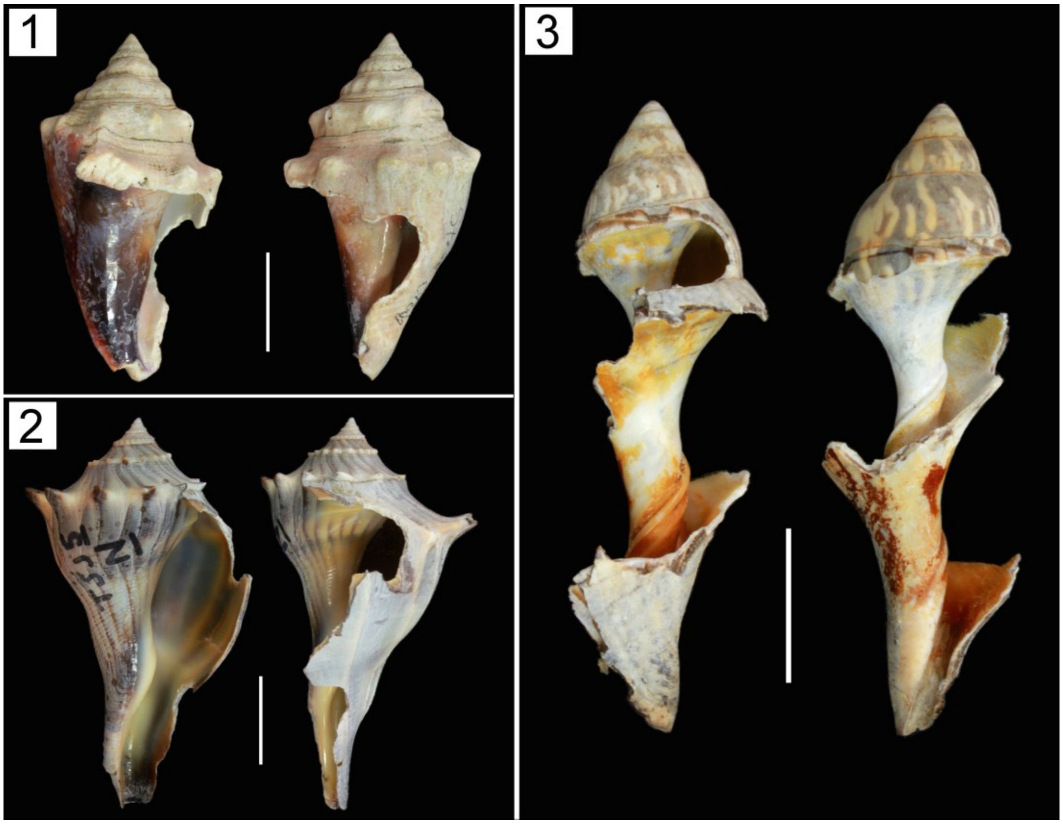

Figure 2-5. Additional modern examples of aperture peeling damage (incipient *Caedichnus spiralis*). *1. Littorina littorea* shell, damaged by *Cancer* sp. in laboratory (Shoals Marine Laboratory, Appledore Island, Maine, USA). Trace extends almost 360° from aperture. Scale bar = 1 cm. *2. Neverita duplicata* shell collected at Wrightsville Beach, NC, USA. Trace extends over 360° from the aperture. Scale bar = 2 cm. Specimens rotated to show extent of damage.

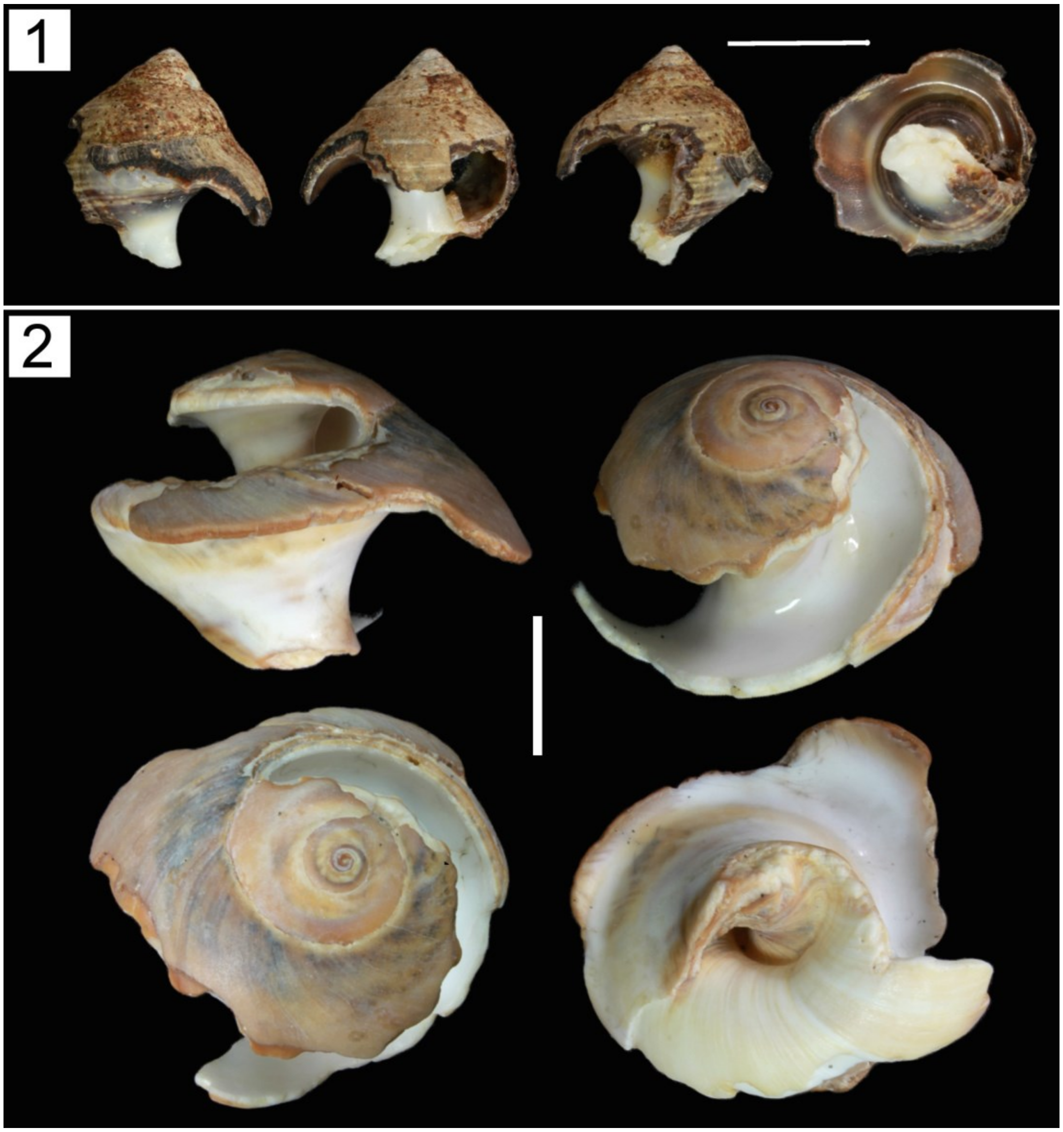

Figure 2-6. Measurement of aspect ratio of predatory aperture damage. H = height of damage parallel to coiling axis; D = depth of damage, measured around the whorl. Aspect ratio equals depth divided by height.

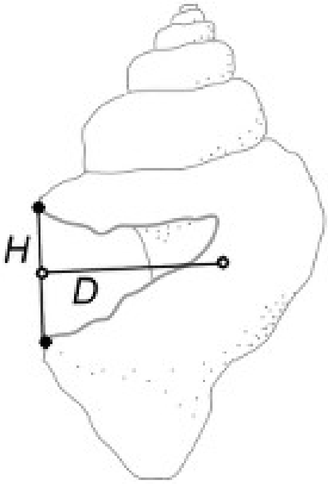

Figure 2-7. *Caedichnus spiralis 1.* Paratype (PRI 68131): *Strombus evergladesensis*, Bermont Formation, lower Pleistocene, collected at Palm Beach Aggregates, Loxahatchee, FL, USA; peeled approximately 450° from aperture. *2*. Paratype (PRI 68132): *Heilprinia carolinensis,* Lower Waccamaw Formation, early Pleistocene, collected at Prince Farm, Columbus County near Old Dock, North Carolina; peeled over 360° from aperture. Scale bars = 2 cm.

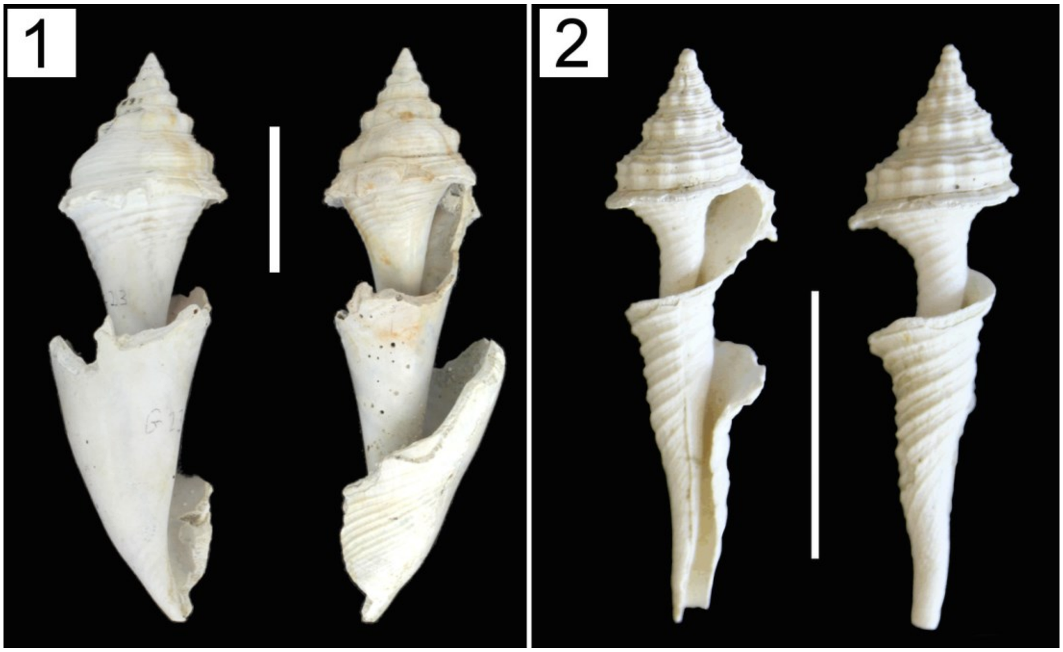

Figure 2-8. *Caedichnus spiralis 1*. Paratype (PRI 68133): *Strombus evergladesensis*, Bermont Formation, lower Pleistocene, collected at Palm Beach Aggregates, Loxahatchee, FL, USA; peeled approximately 360° from aperture. Scale bar = 2 cm. *2*. Paratype (PRI 68134) *Strombus evergladesensis*, Bermont Formation, lower Pleistocene, collected at Palm Beach Aggregates, Loxahatchee, FL, USA; repaired damage over 180° deep. Scale bar = 2 cm. Note the distortions in growth lines and spiral ornament in the regrown shell.

TABLES

Table 2-1. Common types of crushing predation damage on gastropod shells.

Damage Category		Notes	Mechanisms
Complete fragmentation	ig. 2-3.1	Predators large and/or powerful relative to prey May be confused with abiotic damage Unlikely to result in repair scars	Decapod claws Stomatopod hammer Fish jaws Bird gizzard Tetrapod jaws
Spire damage	ig. 2-3.2	Predators smaller and/or less powerful Likely to co-occur with other damage categories Less likely to result in repair scars	rustacean claws or mouthparts
Columella damage	ig. 2-3.2		
Hole in body whorl	ig. 2-3.3		
Aperture chipping	ig. 2-3.4	Predators smaller and/or less powerful May be confused with shell-wedging scars Likely to result in repair scars	rustacean claws or mouthparts Vertebrate jaws or gizzard
Aperture peeling	ig. 2-3.5	Predators smaller and/or less powerful ighly stereotyped, sensitive to relative size/power of predator and prey Likely to result in repair scars	rustacean claws or mouthparts Mammal jaws

Table 2-2. Literature examples that include descriptions or photographs of aperture damage caused by crushing predators on gastropod shells. Predator genera are brachyuran crabs and prey are live gastropods, unless noted otherwise: cf = crayfish; hm = hermit crab; lb = lobster; mm = mammal; pr = prawn; sl = spiny lobster; st = stomatopod; tl = teleost fish. Asterisks indicate which preys are depicted in photos and which predator(s) caused the depicted damage. The damage types described in each paper are listed: cr = outright crushing; sp = spire or apex damage; cm = columella or siphonal canal damage; ap = aperture lip damage; pl = peel; pl* = peel without damage to the aperture lip; hl = hole in shell. Journal abbreviations: JEMBE = Journal of Experimental Marine Biology and Ecology; MEPS = Marine Ecology Progress Series. For full references, see Appendix.

Predator(s)	Prey	cr	sp	cm	**ap**	**pl**	hl	Reference
*Calappa**	*Clibinarius** (hm) in *Fasciolaria* shell					**pl**		Shoup, 1968 Science 160:887-888
*Calappa**	*Pagurus** (hm)					**pl**		McLean and Mariscal, 1973 Experimentia 29:128-130
Calappa, Portunus**	*Umbonium**				**ap**	**pl**		Ogaya, 2004 Paleontological Research 8:311-324
Callinectes	*Bittiolum, Astyris*	cr				**pl**		Cote et al., 2001 JEMBE 264:189-208
Callinectes	*Clibinarius* (hm) in various shells	cr				**pl**		Borjesson & Szelistowski, 1989 JEMBE 133:213-228
Callinectes	*Littoraria*	cr	sp		**ap**			Schindler et al., 1994 Oecologia 97:49-61
Callinectes	*Littorina*		sp		**ap**			Hamilton, 1976 Bulletin of Marine Science 26:403-409
Callinectes	*Pagurus* (hm)	cr	sp		**ap**			Buckley & Ebersole, 1994 JEMBE 182:49-64
*Callinectes**	*Rapana**	cr	sp	cm	**ap**	**pl**		Harding, 2003 JEMBE 297:161-177
Cancer	*Ceratostoma*		sp		**ap**			Donovan et al., 1999 JEMBE 43:59-64
Cancer	*Littorina*			cm		**pl**		Stefaniak et al., 2005 JEMBE 327:103-114
Cancer	*Nucella, Littorina*	cr	sp		**ap**			Lawton & Hughes, 1985 MEPS 27:143-154
Carcinus	*Littorina*	cr				**pl**		Buschbaum et al., 2007 MEPS 329:123-130
Carcinus	*Littorina*	cr	sp			**pl**		Elner & Raffaelli, 1980 JEMBE 43:151-160
Carcinus	*Littorina*					**pl**		Heller, 1976 J of Zoology, London 179:201-213
Carcinus	*Littorina*	cr				**pl**		Rangeley & Thomas, 1987 JEMBE 108:191-197
Carcinus	*Littorina*	cr		cm	**ap**			Rochette et al., 2007 MEPS 330:179-188
Carcinus	*Nucella*	cr	sp	cm	**ap**			Hughes & Elner, 1979 J of Animal Ecology 48:65-78
Carcinus, Portunus, Cancer	*Gibbula, Nucella*	cr			**ap**	**pl**		Muntz et al., 1965 J of Animal Ecology 34:315-329
Carcinus, Portunus, Cancer	*Nucella*	cr	sp	cm	**ap**			Ebling et al., 1964 J of Animal Ecology 33:73-82
*Carcinus**	*Littoraria**	cr			**ap**			Edgell & Rochette, 2009 JEMBE 382:1-7
*Carcinus**	*Pagurus** (hm)					**pl**		Pechenik et al., 2001 JEMBE 262:75-89
*Carpilius**	*Cittarium*, Trochus**					**pl**		Vermeij, 1976 Nature 260:135-136
Carpilius, Daldorfia*, Cancer*, Calappa*, Panulirus** (sl)	*Cittarium*, Trochus*, Cerithium*, Cypraea*, Drupa*, Conus*, Strombus*, Morula*, Nassa*, Fusitriton*, Thais*, Ceratostoma*, Cantharus*, Triumphis*, Cymia*, Terebra*, Muricanthus*, Opeatostoma**		sp	cm	**ap**	**pl**	hl	Vermeij, 1978 *Biogeography and Adaptation: Patterns of Marine Life*
Daldorfia, Carpilius, Eriphia, Cancer*	*Drupa*, Cymatium, Strombus, Conus, Trochus, Nerita, Clypeomorus, Ceritheum, Thais, Amphissa*	cr	sp			**pl**	hl	Zipser & Vermeij, 1978 JEMBE 31:155-172
*Eriphia**	*Nerita*, Planaxis**	cr	sp			**pl**		Shigemiya, 2003 J of Zoology, London 260:259-265
Eriphia, Calappa*, Rattus* (mm)	*Ceratostoma (Ocenebra)*, Gibbula*, Gourmya*, Murex*, Sphaeronassa*, Hinia*, Diogenes* (hm) in various shells		sp			**pl**		Rossi & Parisi, 1973 Bolletino di Zoologia 40:117-135
Gecarcinus, Cardisoma, Rattus (mm), raccoons	*Cerion*	cr	sp		**ap**	**pl, pl***	hl	Quensen & Woodruff, 1997 Functional Ecology 11:464-471
Gecarcinus, rat	*Cerion*	cr				**pl**		Woodruff, 1978 Malacologia 17:223-239
Gonodactylus (st)	hermit crabs		sp			**pl**	hl	Bertness, 1982 JEMBE 64:159-187
Hemigrapsus	*Littorina*				**ap**	**pl**		Bourdeau & O'Connor, 2003 Northeastern Naturalist 10:319-334
Hemigrapsus, Carcinus	*Littorina*					**pl**	hl	Teck, 2006 Unpublished Masters thesis, University of New Hampshire
Hemigrapsus, Lophopanopeus, Cancer	*Littorina*	cr				**pl**		Behrens Yamada & Boulding, 1996 JEMBE 204:59-83
Hemigrapsus, Lophopanopeus, Cancer	*Littorina*	cr				**pl**		Behrens Yamada & Boulding, 1998 JEMBE 220:191-211

Predator(s)	Prey	cr	sp	cm	**ap**	**pl**	hl	Reference
Homarus (lb), _Callinectes_	_Pagurus_ (hm)	cr				**pl**		Weissberger, 1995 Crustaceana 68:739-750
_Homarus_* (lb)	_Buccinum_*				**ap**	**pl**		Thomas & Himmelman, 1988 JEMBE 115:221-236
Macrobrachium (pr)	gastropods				**ap**			Covich, 2010 Hydrobiologia 653:191-215
Menippe, Panopeus, Eriphia, Callinectes	_Cerithium_*, _Tegula, Stramonita, Morula_	cr	sp			**pl**		Turra et al., 2005 MEPS 286:279-291
_Menippe_*, _Callinectes_*	_Fasciolaria_*		sp		**ap**	**pl**	hl	Dietl et al., 2010 Palaeogeogr Palaeoclimat Palaeoecol 296:174-184
_Menippe_*, _Hepatus_*	_Pagurus_* (hm)					**pl**	hl	Brooks & Mariscal, 1985 JEMBE 87:111-118
Micropanope	_Strombus_	cr	sp		**ap**	**pl**		Ray-Culp et al., 1999 JEMBE 240:303-321
Orconectes (cf)	_Amnicola, Gyraulus, Physella, Helisoma_					**pl**		Brown, 1998 Freshwater Biology 40:255-260
Orconectes (cf), _Lepomis_ (tl)	_Physa_	cr			**ap**			DeWitt et al., 2000 Evolutionary Ecology Research 2:129-148
_Ovalipes_*	_Bulla_*		sp		**ap**	**pl**		du Preez, 1984 JEMBE 84:55-71
Ozius, Eriphia	hermits in various shells	cr				**pl**		Bertness, 1981 Ecology 62:411-425
Ozius, Eriphia	hermits in various shells	cr	sp	cm		**pl**		Bertness & Cunningham, 1981 JEMBE 50:213-230
_Ozius_*	_Bembicium_*, _Nerita_*	cr	sp			**pl**		Chilton & Bull, 1986 Marine Biology 93:475-480
Pachygrapsus	_Cerithidea_	cr	sp			**pl, pl***		Sousa, 1993 JEMBE 166:19-37
Pacifastacus (cf)	_Lymnaea_					**pl**		Nyström & Pérez, 1998 Hydrobiologia 368:201-208
Panulirus	_Strombus_					**pl**		Randall, 1964 Marine Science of the Gulf and Caribbean 14:246-295
Panulirus (sl)	_Pagurus_ (hm)	cr	sp			**pl**		McLean, 1983 JEMBE 64:63-74
Panulirus (sl)	_Chlorostoma, Lunella_				**ap**	**pl**		Takahashi et al., 1995 Crustaceana 68:146-150
Petrochirus (hm)	_Strombus_	cr			**ap**			Iversen et al., 1986 Bulletin of Marine Science 39:61-75
_Platytelphusa_*	_Lavigeria_*, _Spekia, Paramelania, Neothauma_	cr	sp		**ap**	**pl**		West et al., 1991 Evolution 45:589-607
Procambarus (cf)	_Physella, Planorbella_	cr	sp		**ap**			Alexander & Covich, 1991 Biological Bulletin 180:387-393
Rattus (mm)	_Pomacea, Radix_					**pl**		Joshi et al., 2006 Philippine J of Crop Science 31:41-51
_Rattus_* (mm)	_Iberus_*					**pl***		Moreno-Rueda, 2009 Evolutionary Ecology 23:463-471
_Rattus_* (mm)	_Planorbarius_*, _Viviparus_*					**pl, pl***		Parisi & Gandofi, 1974 Bolletino di Zoologia 41:87-106
Shelduck *	_Hydrobia_*				**ap**			Cadee, 1994 Paleontology 37:181-202
Shelduck*, shore crab*	_Hydrobia_*				**ap**	**pl**		Cadee, 2011 Palaios 26:245-249
Somaniathelphusa	_Biomphalaria, Physella, Radix, Melanoides_		sp		**ap**			Dudgeon & Cheung, 1990 J of Zoology, London 220:147-155
spiny lobsters	gastropods				**ap**			Kent, 1979 Crustaceana Supp. No. 5 pp. 142-146

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APPENDIX. Full references for Table 2-2.

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CHAPTER 3
GASTROPOD SHELL REPAIR TRACKS PREDATOR ABUNDANCE[2]

INTRODUCTION

Predation is a major factor in the structure of ecosystems, influencing biological diversity and trophic relationships in ecological communities. Due to the logistical challenges of observing predatory activity directly in marine environments, predation traces, such as repair scars, have been used as a proxy for predation intensity (Raffaelli, 1978; Kowalewski et al., 1997; Alexander and Dietl, 2003). Repair scars provide a quantitative record of predator-prey encounters in the form of failed predatory attacks (Alexander and Dietl, 2003); however, studies testing the validity of repair frequency (the proportion of a population that bears repair scars) as a proxy for predation mortality (the proportion of the population killed by predators) or attack frequency (the proportion of the population attacked by a predator, regardless of outcome) are generally lacking. What factors influence the frequency of predation traces in a prey population? Does repair frequency provide an accurate representation of attack frequency and/or prey mortality? We address these questions directly by examining the relationship between repair scars on *Chlorostoma funebrale* (Adams 1855) gastropods on rocky intertidal shores of Vancouver Island, British Columbia and multiple independent variables, including prey size and shell thickness, predatory *Cancer productus* (Randall 1839) abundance, and local water velocity.

A variety of approaches are commonly employed to examine predation in modern environments, depending on the nature of the study. Direct observation of predatory interactions in the field can provide detailed, accurate data about the behavior of both predator and prey during an attack, but such intensive fieldwork may not be practical for studies of broad geographic scope. Laboratory-based observations of predatory interactions are utilized when the hypotheses require direct observations or control over physical conditions (e.g., Grubich, 2000; Herrel and Holanova, 2008; see Stafford *et al*. [*accepted with revisions*] for examples involving aperture-peeling predators on gastropod-shelled prey). Unfortunately, inferences may be limited in application because predator or prey behavior can be influenced by captivity.

In situ predator-exclusion caging and prey tethering experiments are used to estimate prey mortality via short-term monitoring of a representative group of the prey population. The

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[2] A version of this chapter is in press. Stafford et al., *Marine Ecology*

data are derived directly from organisms in their natural environments. Tethering has been criticized, however, as it may alter the vulnerability and behavior of prey organisms (Barbeau and Scheibling, 1994; Zimmer-Faust et al., 1994; Kneib and Scheele, 2000). Due to the logistic limitations of caging and tethering protocols, these techniques are appropriate only for examining predation on local scales, over short time periods (Aronson et al., 2001); the validity of extrapolating these data to larger spatial or temporal scales is debatable.

Predation proxies (variables that correlate with mortality or attacks) are useful when research requires large amounts of quantitative data derived directly from natural populations over broad geographic regions or repeated sampling over longer time scales. Predator population censuses have been used to infer predation intensity (i.e., prey mortality); communities with larger and/or more abundant predators are expected to experience stronger pressure (Raffaelli and Hughes, 1978; Raffaelli, 1982; Boulding and Van Alstyne, 1993; Leonard et al., 1998; Boulding et al., 1999; Robles et al., 2001). Morphological defensive prey characteristics, such as thick shells or prominent spines, may reflect predation intensity, as better-defended shells can be a genetic or plastic response to greater predation pressure (Vermeij, 1977a; Palmer, 1979; Trussel, 2000). Note, however, that shell characteristics are also influenced by non-predatory factors (e.g., water chemistry, temperature) (Tyler et al., 2014).

Non-fatal shell-crushing attacks on heavily biomineralized organisms, such as mollusks and brachiopods, can leave repair scars, distortions of the growth lines where the prey has replaced damaged material (Alexander and Dietl, 2003). Predatory repair scars on the shells of molluscs and brachiopods are easy to observe, provide large amounts of quantitative data, and are preserved after the prey dies. Repair scars are used to examine predation in modern ecosystems (e.g., Schindler et al., 1994; Cadée et al., 1997; Kowalewski et al., 1997; Moody and Aronson, 2012), and in the paleontological literature, where such traces are often the only direct evidence of predator-prey interactions (Vermeij, 1987; Kowalewski, 2002; Leighton, 2002; Harper, 2006; Stafford et al. [accepted with revisions]). Scars accumulate throughout an organism's lifetime, averaging out the "noise" of short-term ecological fluctuations that can obscure trends in predation.

Although repair scars can provide quantitative, high-resolution data from multiple localities or environments, the relationship between repair scars (a measure of failed attacks) and predation mortality (a measure of fatal attacks) is ambiguous (Leighton, 2002; Alexander and

Dietl, 2003). Higher frequencies of repairs may suggest two contrasting scenarios: (A) the frequency of attacks is higher, although the success rate of the attacks is unchanged; or (B) the frequency of attacks is unchanged, but the attacks that do occur are more likely to fail. In terms of predation intensity, the first scenario implies higher mortality (more attacks lead to more kills), while the second scenario implies lower mortality (more failed attacks lead to fewer kills). It is important to distinguish between changes in attack frequency and attack success when considering how and to what degree predation influences the prey population. Parsing the relationship between repair scars and predation intensity could confirm the validity of using repair frequency as a proxy for predation intensity in prey populations.

Cadée et al. (1997) found that repair frequency varied with environment and as a result argued that repair frequency is not a reliable indicator of predation. However, this environmental variation may have meaningful consequences for predators and prey, as environmental conditions can have an important influence on the abundance and behavior of organisms. Menge and Sutherland (1987) suggested that predation should be a dominant factor in community structuring in environments with low environmental stress, but that the role of predation is greatly reduced when environmental stress is high. This prediction has been borne out in numerous observations of predation in the rocky intertidal: crab predation on gastropods is greater in low-wave-energy habitats (Kitching et al., 1966; Heller, 1976; Boulding et al., 1999). Wave exposed environments can be inhospitable to predatory crustaceans, as high wave energy can make it difficult for them to forage; quiet-water, protected environments allow these predators to flourish, resulting in greater predation intensity (Raffaelli, 1978; Leonard et al., 1998; Boulding et al., 1999; Robles et al., 2001; Freeman and Hamer, 2009). If repair frequency is a function of attack frequency, repairs should track predatory crab density. Alternatively, if repair frequency is a function of predator success and failure, then repair frequency may be driven by shell defenses; enhanced shell defenses can reduce mortality, with more failed attacks resulting in more repairs. Habitats with better-defended populations (i.e., thicker or taller shells) would have greater repair frequencies.

Because low energy habitats typically have a greater abundance of predators, greater attack frequencies, and better-defended prey, identifying the primary driver of repair frequency is not as simple as correlating repair frequency with environment. We employ a two-part analysis: First, we test whether the repair frequency differs between wave protected and wave exposed localities; this approach not only directly tests this important assumption, but also tests whether repairs are a valid predictor of predation pressure Second, to identify the primary factor influencing repair frequency, we examine whether the likelihood of an individual having a repair scar ("repair occurrence") can be predicted by shell morphology (height and/or thickness), predator abundance, and/or environmental conditions (water velocity) using Binomial Logistic Regression. If shell height and/or thickness are the strongest variable in predicting repair occurrence, this indicates that predator success drives repair frequency. In contrast, if predator abundance is the most significant variable in predicting repair occurrence, this indicates that attack frequency drives repair frequency, and thus repair frequency is a valid proxy for predation intensity in the system.

MATERIALS AND METHODS

Repair surveys were conducted on the intertidal gastropod *Chlorostoma funebrale* at six localities (three wave-protected and three wave-exposed) near Bamfield Marine Sciences Centre on Vancouver Island, British Columbia, Canada (48.8303° N, 125.1375° W). The study area is located on the southern side of Barkley Sound, on the central west coast of Vancouver Island (Figure 3-1A). The intertidal habitats tend to be rocky, with a typical suite of Pacific Northwest organisms including red, brown, and green algae, barnacles, mussels and other bivalves, sea stars, shore crabs (*Hemigrapsus* spp.), rock crabs (*Cancer* spp.), several types of snails, and hermit crabs.

Study Species

Chlorostoma funebrale (Family Turbinidae; formerly *Tegula funebralis*) is a globose gastropod with a round aperture, ~10-30 mm shell height in our study area. *Ch. funebrale* has a thick shell with no ornament (Figure 3-2A) and tends to aggregate at the bases of boulders, among cobbles, and in rocky tidepools (Frank, 1975). It is one of the most abundant gastropods in the rocky intertidal habitats of the region, and it inhabits both wave-protected and wave-exposed settings. *Ch. funebrale* individuals can be extremely long-lived, producing shell (and retaining scars) for up to 30 years (Frank, 1975), and are thus an ideal species for studying repair scars caused by crushing predation.

Cancer productus crabs are abundant in the rocky habitats shared with *Ch. funebrale*. *Ca. productus* prey upon *Ch. funebrale*, among other molluscs, using their powerful chelae to crush the prey shell (see below, “Predator Abundance”).

Study Localities

To capture the variation in crushing predation pressure observed previously in similar environments (Boulding et al., 1999), we collected data at three wave-protected localities and three wave-exposed localities (Figure 3-1B; Table 3-1), examining gastropods living at 1-2 m above datum. Wave-protected habitats are defined, for the purposes of this study, as areas where little to no waves occur, and maximum water velocities are driven by tidal currents. The protected sites are located within inlets or on the landward side of an island, and are thus sheltered from large waves; water movement is due primarily to tides. The exposed sites face the open water of Barkley Sound and thus experience significant wave forces. Because wave-exposed habitats are less favorable for crushing predators (Robles et al., 2001) and prey organisms may also reduce foraging or seek shelter in response to environmental exposure (Moran, 1985), exposed environments tend to have lower attack frequencies (Leonard, et al. 1998; Boulding et al., 1999).

Repair Occurrence

Our goal is to determine whether variation in repair scars is driven by predator attack frequency or by predator success. This was done in two parts, first by determining whether repair frequency differed between wave protected and wave exposed habitats, and second by examining what factors contribute to the likelihood of an individual having a repair scar (repair occurrence). Repair data were collected over the course of four summer field seasons (2009 – 2012). At each locality we examined a representative subsample of the *Ch. funebrale* population for repair scars, comprising a minimum of 100 individuals per locality. Repair scars manifest as jagged disruptions in the shell surface that are not parallel to the growth margin (Alexander and Dietl, 2003; Stafford et al. [accepted with revisions]) (Figure 3-2B).

The frequency of repair was compared for each locality to determine whether the occurrence of scars differed between protected and exposed sites. The repair frequency is calculated by dividing the number of individuals with at least one scar by the total number of individuals, resulting in a number between 0 and 1.

To determine what factors contribute to the likelihood of an individual having a repair scar (repair occurrence: the binary response variable of repair scar presence or absence per individual), the following variables were recorded and measured: for each individual, shell height and shell thickness at the aperture; and at each locality, predator abundance and maximum water velocity.

Morphology

We measured shell height (the distance between the shell apex and the anterior margin of the apertural lip, parallel to the shell coiling axis) and shell thickness (at the posterior-most point on the outer apertural lip) using digital calipers (±0.002 mm) (Table 3-2). Shell height is a common proxy for overall gastropod size. Although "size" is a rather non-specific quality, it can convey important information to the predator: larger individuals offer more edible tissue, but their shells are typically thicker and more difficult to break (Boulding, 1984; Boulding and LaBarbera, 1986). Larger shells are also probably older, and thus have had more time to accumulate repairs (Vermeij, 1987; Dietl and Kosloski, 2013).

Thicker shells can lead to increased occurrences of repairs by decreasing the fatality rate of predatory attacks, as thicker gastropod shells can typically withstand greater and repeated loading (Boulding, 1984; Boulding and LaBarbera, 1986). Thicker shells may take more time or strength for crabs to break, increasing the probability that the crab will give up the attack or accidentally drop the prey, allowing the prey to survive and repair its damaged shell (Elner and Raffaelli, 1980). Longer handling times also increase predators' exposure to their own predators (Boulding, 1984).

Predator Abundance

We recorded the occurrence of *Cancer productus*, the major invertebrate crushing predator in the system (Table 3-1). *Ca. productus* (adult carapace width up to 20 cm; 15 cm was more typical for crabs observed in this study) is abundant on rocky coasts of the Pacific Northwest, and has robust chelae with molariform dentition typical of crushers. While *Ca. productus* is not as specialized for crushing as many tropical crab lineages (Vermeij, 1977b), it is a strong and voracious predator of molluscs and is capable of generating crushing forces approaching 200 N (Boulding, 1984; Taylor, 2001). During daylight high tides, we censused the *Ca. productus* populations at each locality by dropping baited crab rings to various depths for ten-minute intervals (Table 3-1). We repeated this ten to 20 times at different locations within each locality. The censuses may be biased toward larger adult crabs, which are more active during daylight than younger, smaller crabs (Robles et al., 1989). Because larger crabs attack and consume more prey, a census biased toward larger individuals is more likely to be a reasonable proxy for crab attacks. We also noted any crabs observed during our gastropod repair surveys, although these crabs were not caught and measured. Census data were consistent with our observations of crab abundance. The reported values indicate the mean number of crabs caught per 20 ring drops for each locality (Table 3-1).

Other predatory crabs in the region include *Metacarcinus* (formerly *Cancer*) *magister* (Dana, 1852) and the invasive European *Carcinus maenas* (Linnaeus, 1758). Neither of these species were caught nor observed during our surveys. *Hemigrapsus* spp. (shore crabs) are known to crush small gastropods (less than 10 mm shell height, such as *Littorina* spp.), but are unlikely to pose a threat to adult *Ch. funebrale* (Behrens Yamada and Boulding, 1998).

Maximum Water Velocity

Stronger wave conditions are associated with decreased crushing predator activity (Boulding et al., 1999; Robles et al., 2001; Freeman and Hamer, 2009). Average maximum water velocities (i.e., the average of daily maximum velocities) from each site were gathered from the literature (Bates et al. unpublished dataset via A.R. Palmer, personal communication; Robles et al., 1989; Marchinko and Palmer, 2003; Neufeld and Palmer, 2008) (Table 3-1). Velocities at wave-exposed sites were generally measured using drogues, while wave-protected sites were measured using velocimeters. Velocities in protected environments were not high enough to be measured by drogues, while the waves at exposed sites were too dangerous to use hand-held velocimeters. This protocol difference is unlikely to pose a problem, as the exposed velocities were orders of magnitude greater than the protected velocities. The relative water velocities drawn from the literature are consistent with our personal observations of the relative energy conditions of the localities during our surveys (Table 3-1).

Data Analysis

We performed a Fisher's exact test to determine whether repair frequency differed significantly between protected sites and exposed sites.

We then tested whether the binary response variable, repair occurrence, was affected by any of the following independent variables: shell height, lip thickness, crab abundance, and water velocity. Binary Logistic Regressions (BLR, Hosmer and Lemeshow, 2000) is suitable for binary response data, i.e., "repaired" = 1 or "not repaired" = 0. BLR tests the distribution of the data against a logistic, rather than linear curve, accounting for the non-continuous nature of the response variable. Rather than a typical R^2 value (as is produced by Multiple Linear Regression), BLR produces a "max-rescaled R^2" value to indicate the proportion of variation explained by the model. The max-rescaled R^2 is adjusted to a 0-1 scale and is a more meaningful and intuitive measure of the variation explained by the model (due to the nature of the logistic curve, the typical R^2 may not fall within the 0-1 range). BLR was repeated for two models, using both regular BLR and stepwise BLR. The better explanatory model was assessed based on significance (the model's Wald statistic and p-value) and model support (Akaike Information Criterion, or AIC). Within the better model, we identified the most important explanatory variable, based on the variable's Wald statistic and associated p-value. BLR was performed using SAS 9.3 (SAS Institute, Carey, NC) using "PROC LOGISTIC".

We also performed a Pearson's Product Moment Correlation between repair frequency (the proportion of individuals bearing at least one repair scar) and the best explanatory variable to confirm the relationship.

RESULTS

The resulting data matrix consisted of 870 individuals, of which 546 had at least one repair scar (Table 3-1). The Fisher's exact test showed that repair frequency was significantly greater at the three protected sites compared to the three exposed sites ($p \ll 0.0001$).

A stepwise BLR was performed using all explanatory variables (wave height, crab density, shell height, and shell thickness) and their interaction effects. As no interaction effects were significant in the stepwise model, a complete model was fit using the main effects only (Table 3-3; Wald stat. = 84.77, $p < 0.0001$, AIC = 1056.78, max-rescaled $R^2 = 0.151$). The complete fit model (using main effects only) had a lower AIC than the stepwise model including interaction effects, and was therefore identified as the better-supported model. Crab abundance had the greatest explanatory contribution to the complete fit model (Wald stat. = 11.20, p = 0.0008), while the other three variables (water velocity, shell height, and shell thickness) made significant but weaker contributions (Table 3-4).

The Pearson's Product Moment Correlation showed a significant correlation between repair frequency (proportion of individuals bearing at least one repair scar) and crab abundance per locality (r = 0.837, df = 4, p = 0.038) (Figure 3-3).

DISCUSSION

The Fisher's exact test demonstrated that repairs occurred significantly more frequently at protected, compared to exposed, environments (see also Figure 3-3). If repairs are interpreted as a proxy for predation intensity, our findings are consistent with Boulding et al. (1999), where attack frequency and mortality were found to be greater in wave-protected habitats in the Bamfield area. This interpretation is corroborated by the BLR analysis; crab abundance is the most important factor in explaining repair occurrence among *Chlorostoma funebrale*. These results suggest that repair occurrence is most heavily influenced by attack frequency (a function of predator abundance), rather than predator success (a function of prey defensibility). While the explanatory contributions of shell thickness, shell height, and water velocity are significant, their effects are decidedly minor compared to that of predator abundance.

There are a number of reasons why attack frequency may play a dominant role over attack success in this predator-prey system. The predator, *Cancer productus*, is an order of magnitude larger than the prey gastropods in this study, and thus has an immense strength advantage over the prey's shell defenses. In a laboratory setting, we have observed adult *Ca. productus* (approximately 13 cm carapace width) completely crush *Nucella lamellosa* (30 mm shell height), snails which are substantially larger than most *Ch. funebrale*. Researchers have reported *Ca. productus'* crushing forces approaching 200 N (Boulding, 1984; Taylor, 2001). Many crabs can also crush prey that seem to exceed their abilities by repeatedly squeezing the shell to induce fatigue damage (Boulding and LaBarbera, 1986) or using alternative shell attack methods, such as aperture peeling (Zipser and Vermeij, 1978; Elner and Raffaelli, 1980; West et al., 1991; Preston et al., 1996).

The variation observed in *Ch. funebrale* shell size and thickness is unlikely to have a population-scale effect on the *C. productus'* attack success frequency. These results are relevant when considering similar intertidal systems with shell-crushing predators and gastropod prey, as predators tend to be substantially larger than their prey (i.e., organisms in a lower trophic level (Jennings et al., 2001). The predators' extreme size and strength relative to the prey appear to overshadow the influence of prey defenses on repairs. Instead, instances of prey survival and repair are due to factors unrelated to prey defense, and thus repair frequency varies as a function of attack frequency and is proportional to prey mortality.

The low explanatory power of the BLR models (max-rescaled R^2 approximately 15%) is not uncommon in biological systems, where innumerable variables interact in complex and sometimes redundant ways. Other variables not examined in this study (e.g., temperature, salinity, primary productivity, competition) may also contribute to repairs. However, as some of these variables presumably would also influence crab density, for which the models do account, it is unclear which other explanatory variables would be important in predicting repairs. Some portion of the unexplained variation in repairs is likely due to chance. When prey organisms are abundant, a given crab is likely to encounter multiple, similar potential prey simultaneously. Our experience with *Ca. productus* foraging suggests that the crabs choose haphazardly from available prey within patches, and may not be capable of distinguishing among similar sized prey (pers. obs.). From a given patch of potential prey, the predator's "choice" may not be explained by any of the variables that distinguish the prey individuals from one another.

Based on our finding that crab abundance drives *Ch. funebrale* repair occurrence as a result of attack frequency, and the fact that variation in *Ch. funebrale* shell morphology has little influence on the likelihood of an individual having a repair scar, it stands to reason that attack frequency is itself a proxy for predation mortality, at least in this system.

Cadée et al. (1997) noted that variations in microhabitat, shell morphology, or behavior, tend to lead to variation in repair scar occurrence. However, consistent with Schindler et al. (1994), who demonstrated results similar to ours in a different crab-prey system from Georgia, USA, we find that variation in repair frequency is predictable. Specifically, repair frequency may vary with environment or predator behavior, and this variation ultimately alters the frequency of attacks, either by affecting the population of the predator or by affecting the predator's ability or time to forage. We found that repair frequency is a proxy for attack frequency, regardless of environment or behavior, and thus may provide insight into the relationship between environment and predation. For example, a decrease in repairs of prey through time at a given location may suggest that environmental conditions for the predator have deteriorated (leading to fewer predators and lower attack frequencies). Additional studies targeting other predator and prey taxa, habitat types, geographic regions, and hydrodynamic regimes are required to determine the generality of these results.

CONCLUSIONS

Repair scar frequency is a powerful tool for assessing crushing predation intensity on marine gastropod populations. We observed that crab abundance was a dominant factor in predicting repair scar occurrence, followed by shell thickness and height, and water velocity. The strong influence of crab abundance on prey repairs indicates that predation by crabs may be a driving force in these rocky intertidal communities. As crab abundance is an indicator of attack frequency, we conclude that repair frequency is a valid proxy for prey mortality. This study confirms the value of repairs as used in previous ecological and paleontological research, and furthermore illustrates the potential of this method for evaluating predation intensity among environments, across geographic gradients, and through time.

FIGURES

Figure 3-1. A. Location of study area near Bamfield, British Columbia, within Barkley Sound on the west coast of Vancouver Island. B. Study localities near Bamfield Marine Sciences Centre. Wave-exposed localities: BB = Brady's Beach, SB = Scott's Bay, DE = Dixon Island Exposed; Wave-protected localities: DP = Dixon Island Protected, SP = Strawberry Point, GI = Grappler Island.

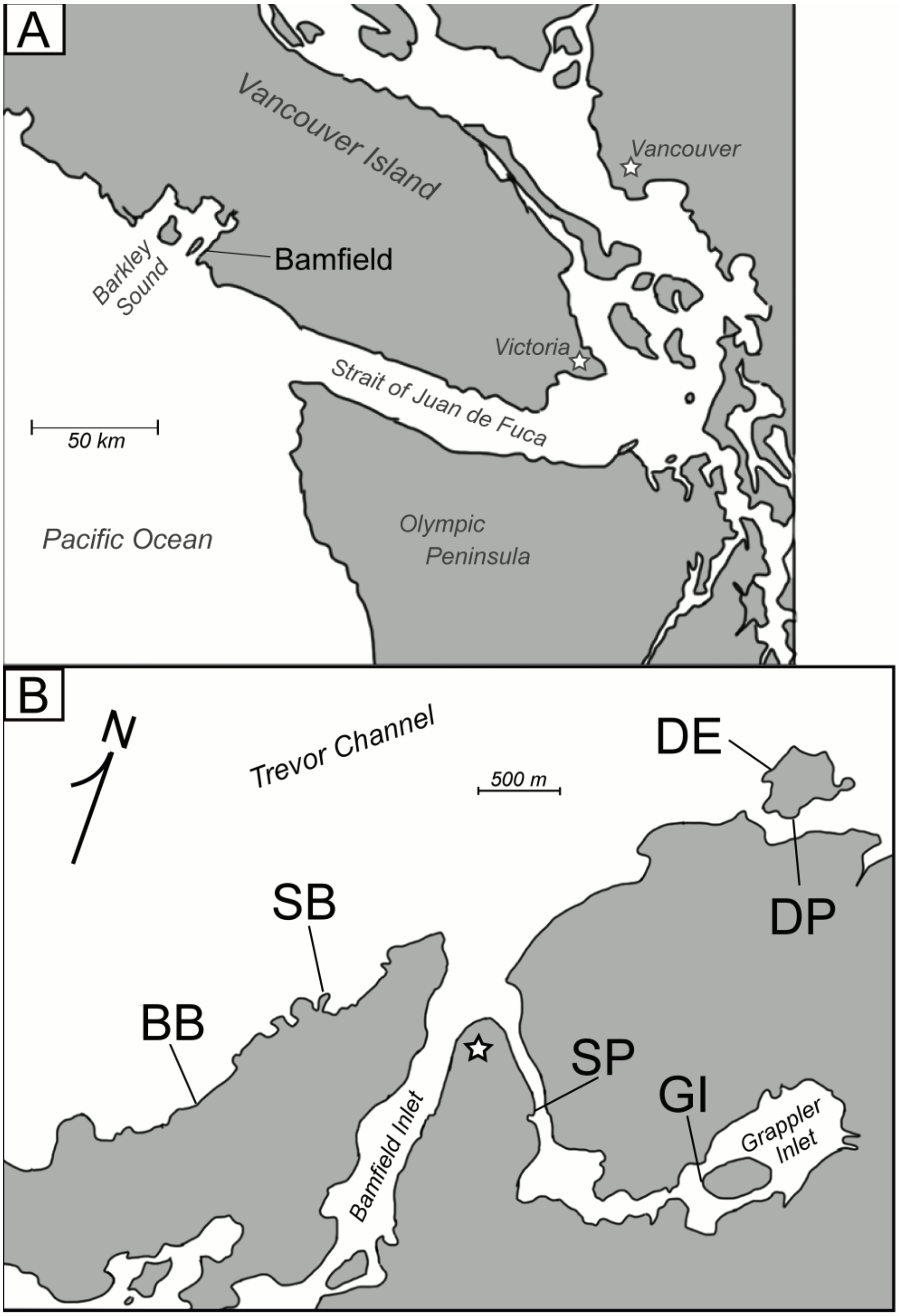


Figure 3-2. A. *Chlorostoma funebrale*. B. *Ch. funebrale* showing prominent repair scar. Scale bar = 10 mm.

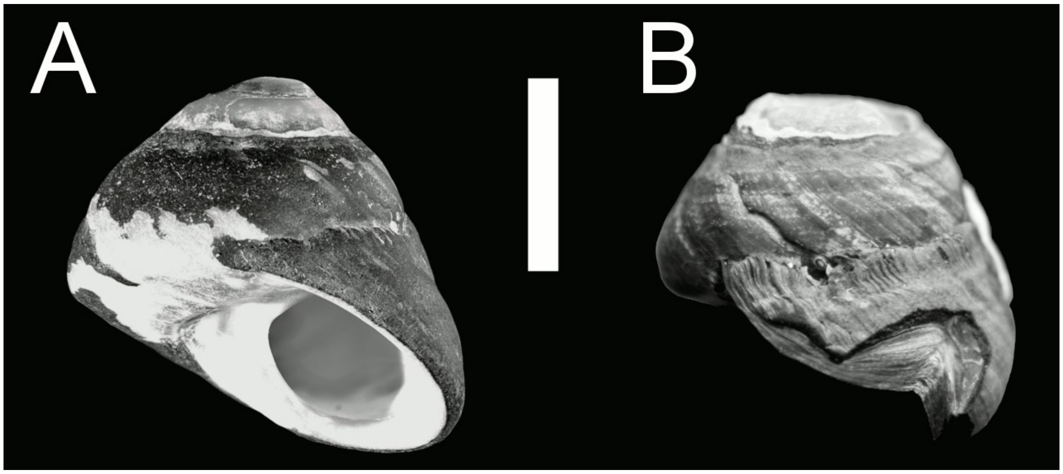
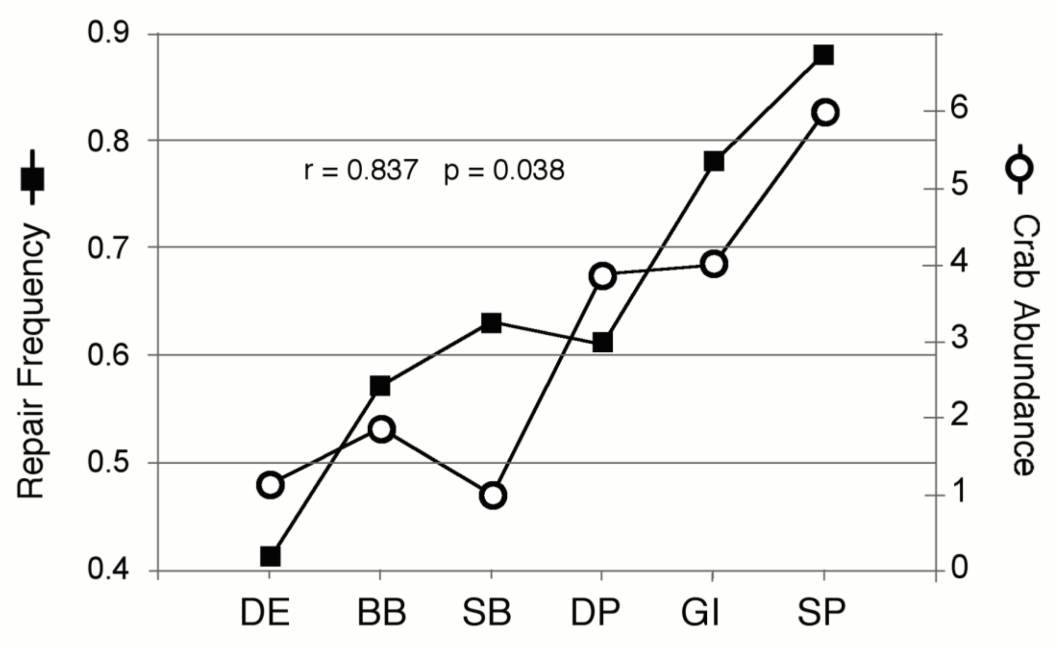


Figure 3-3. Relationship between crab abundance (crabs / 20 capture-attempts) and repair frequency (proportion of individual gastropods with at least one repair). Exposed sites on the left (DE = Dixon Island Exposed, BB = Brady's Beach, SB = Scott's Bay) and wave-protected sites on the right (DP = Dixon Island Protected, GI = Grappler Island, SP = Strawberry Point). Pearson's product moment correlation: r = 0.837, p = 0.037.



TABLES

Table 3-1. Summary of variables for the three exposed and three protected study localities: V = maximum water velocity measured in m/s; Crabs = average number of crabs per 20 10-minute crab-ring drops; Depth = range of depths sampled with crab rings, in meters; and the total gastropod specimens examined at each locality.

Locality	v (m/s)	crabs/10 min	depth (m)	total gastropods
Brady's Beach	5.00	1.87	0.25-2.5	100
Scott's Bay	1.85	1.00	0.25-4.0	230
Dixon Exposed	1.75	1.13	0.25-4.0	200
Dixon Protected	0.06	3.88	0.25-4.0	100
Strawberry Point	0.07	6.00	0.25-4.0	140
Grappler Island	0.05	4.00	0.25-2.5	100

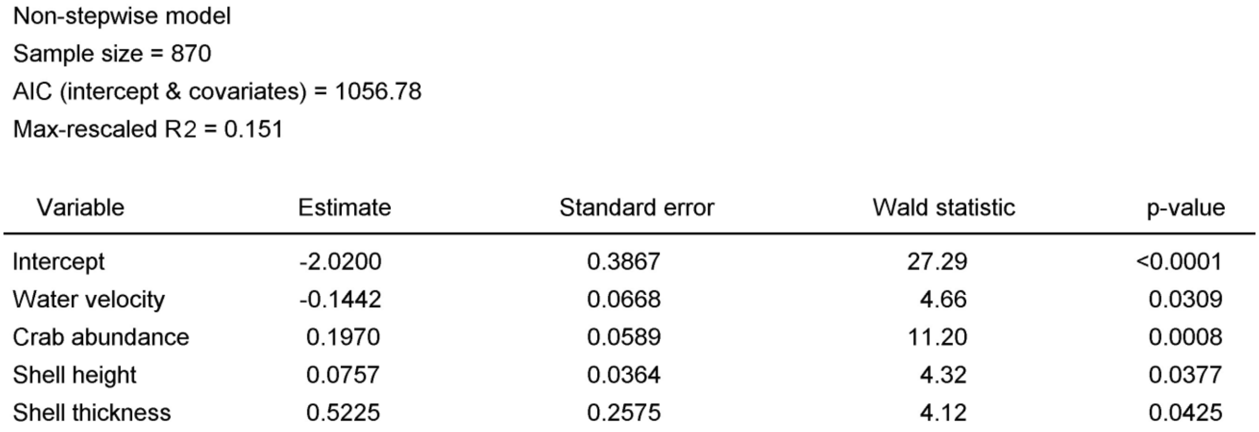
Table 3-2. Mean (standard deviation) shell height and shell thickness, as well as the repair frequency (proportion of specimens bearing at least one repair scar) at each locality.

Locality	height	thickness	repair frequency
Brady's Beach	20.07 (3.95)	2.32 (0.50)	0.57
Scott's Bay	15.51 (3.39)	1.74 (0.51)	0.63
Dixon Exposed	16.00 (2.14)	1.83 (0.33)	0.41
Dixon Protected	18.17 (2.80)	2.31 (0.42)	0.61
Strawberry Point	15.69 (4.58)	2.35 (0.61)	0.88
Grappler Island	17.17 (3.20)	2.37 (0.49)	0.78

Table 3-3. Summary of BLR models.

	Stepwise	AIC (intercept & covariates)	R^2 (max-rescaled)	Wald statistic	p-value
1. shell thickness + crab abundance	yes	1059.96	0.141	80.53	< 0.0001
2. water velocity + crab abundance + shell height + shell thickness	no	1056.78	0.151	84.77	< 0.0001

Table 3-4. BLR table for the preferred model.



Non-stepwise model
Sample size = 870
AIC (intercept & covariates) = 1056.78
Max-rescaled R2 = 0.151

Variable	Estimate	Standard error	Wald statistic	p-value
Intercept	-2.0200	0.3867	27.29	<0.0001
Water velocity	-0.1442	0.0668	4.66	0.0309
Crab abundance	0.1970	0.0589	11.20	0.0008
Shell height	0.0757	0.0364	4.32	0.0377
Shell thickness	0.5225	0.2575	4.12	0.0425

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CHAPTER 4

FORAGING AND HANDLING BEHAVIOR OF A PREDATORY CRAB ON GASTROPOD AND HERMIT CRAB PREY

INTRODUCTION

Most studies examining hermit crab or snail response to predatory cues (visual, mechanical, or chemical) have done so without actually exposing the prey to predation (Bulinski, 2007; Scarratt and Godin, 1992; Hazlett, 1996; Mima et al., 2001; Dalesman and Inchley, 2008). Even less frequently are hermit crab and snail prey made available to crab predators at the same time (two exceptions are Rossi and Parisi, 1973; Bertness and Cunningham, 1981); most studies have examined only one prey item, though such examinations of each type of prey have been extensive. These studies have focused on the response behavior of the prey to various predatory cues (e.g., Bulinski, 2007; Scarratt and Godin, 1992; Hazlett, 1996; Mima et al., 2001; Dalesman and Inchley, 2008), rather than examining the predatory crabs' foraging behavior in the presence of multiple prey types. However, these one-predator-one-prey studies have provided a solid basis for making predictions about the predatory and defensive behavior expected when all three organisms (predatory crabs, hermit crabs, and snails) are allowed to interact freely. The present study examines the behavioral interactions of the predatory *Cancer productus* (Randall, 1839), the snail *Nucella lamellosa* (Gmelin, 1791), and the hermit crab *Pagurus granosimanus* (Stimpson, 1858) (in *N. lamellosa* shells) in an arena-type laboratory setup to determine whether the crabs have a preference for one prey type over another and what behavioral factors influence which prey type is selected.

The hermit crabs and snails that predatory crabs hunt often inhabit the same shells, but each prey has other characteristics that affect their appeal as prey, their availability to the predator, and the costs incurred by the predator in hunting and consuming the prey. The limited research on predatory crabs' hermit crab-versus-snail preference suggests that hermit crabs may be preferable over snails when other factors are equal (Rossi and Parisi, 1973), although Bertness and Cunningham (1981) did not observe any preference. This may be because hermit crab shells tend to be older and weaker than snail shells, so they are easier to crush (Smyth, 1990; LaBarbera and Merz, 1992; Buckley and Ebersole, 1994). Hermit crabs may also be more visually conspicuous (because they are more mobile), and thus more vulnerable to predation independent of shell condition (Rossi and Parisi, 1973). Hermit crabs may be able to counteract this vulnerability by choosing well-defended shells. Rossi and Parisi (1973) found that when the crab predators (*Eriphia verrucosa*) chose between hermit crabs and snails in different species of shell (i.e., the gastropod species that originally occupied the shell), preference for certain shell species overrode any preference for hermit crab prey. Crabs also tend to be indiscriminant foragers, sometimes even attacking objects that merely look like prey (e.g., LaBarbera, 1981), so it is not clear from previous research how finely tuned they are to the differences between hermit crab and snail prey. The magnitude and direction of any prey preferences likely vary by predatory crab species, and even among individuals of the same species.

Review of the literature does suggest that the crushing techniques employed by a given type of crab are broadly the same regardless of prey whether the prey is a live gastropod or hermit crab (Rossi and Parisi, 1973; see Table 2-2 in Chapter 2), although this does not necessarily suggest that the crabs are incapable of distinguishing between prey.

The hermit crabs' position in this trophic triangle is particularly interesting, as their need to acquire new shells may be at odds with anti-predatory strategies. As a hermit crab grows, it must acquire larger shells. The shells that are already in the hermit crab population are often in poor condition, so hermit crabs are always in the market for a higher quality shell (many studies have shown strong preferences by hermit crabs for undamaged shells (Abrams, 1980; Bertness, 1980; McClintock, 1985; Pechenik et al., 2001)). It makes sense, then, that hermit crabs are attracted to the sites of predation on snails: the death of a snail brings a new, maybe pristine shell into the population, and also allows shell trading among the hermit crabs (McLean, 1973; Gilchrist, 1984; Hazlett and Rittschoff, 1997). Hermit crabs have even shown particular attraction to the flesh of certain species of snails (with better anti-predatory shells) (Hazlett and Rittschoff, 1997) and some size specificity (only small hermit crabs will arrive at the kill site of a small snail, as no large shells will become available) (Gilchrist, 1984). The drawback of this attraction to snail kills is that the hermit crabs may expose themselves to their own predators.

Previous research has shown that hermit crabs respond to chemical cues from snail kills (McLean, 1973; Rittschoff et al., 1990; Hazlett and Rittschoff, 1997) (as evidenced by hermit crabs' preference for certain snail species when the species could not be visually ascertained (Gilchrist, 1984)), and to both visual and chemical cues from predatory crabs (Scarratt and Godin, 1992; Hazlett, 1996; Mima et al., 2001; Dalesman and Inchley, 2008). In studies of the interaction of these cues, predator cues tended to dampen hermit crabs' shell-exploring activity (Hazlett, 1996) while multiple predator cues enhanced defensive behaviors (Dalesman and Inchley, 2008). This study aims to explore how the prey's responses to these cues impacts predator behavior and prey preference.

METHODS

Specimens

The two predators used in this experiment were medium-sized (carapace widths 133 mm and 127 mm) male *Cancer productus*, caught together in a star-trap off the dock at Friday Harbor Laboratories. The crabs were dubbed "Rosencrantz" and "Guildenstern". From here on, the unqualified term "crab" refers to the predatory *C. productus*.

I collected 30 *Nucella lamellosa* and 49 *Pagurus granosimanus* in *N. lamellosa* shells from Argyle Creek on San Juan Island. Both the snail and the hermit crab shells were uniformly large. For specimens that were used in the experiment, *N. lamellosa* shell height ranged from 29.02 mm to 42.24 mm and *P. granosimanus* shell height ranged from 26.32 to 44.25 mm.

The quality of shells deteriorates through generations of use by hermit crabs (Walker, 1989; Smyth, 1990; LaBarbera and Merz, 1992), so only the highest quality hermit-inhabited shells were used. Shells missing aperture or apex material, shells with holes, and extensively bored shells were not used. Few of the shells used, hermit crab or snail, would be considered pristine (Figure 4-1). Even among live snails, bioerosion and encrustation were common, including boring worms (Figure 4-1). Thus, the hermit crab and snail shells were similar in terms of quality. Furthermore, the shell quality of both prey types was typical of that found in the local intertidal habitats.

Laboratory setup

The two *C. productus* were each housed in adjacent 90-m by 120-m tanks, in 30 cm of flowing seawater in a laboratory room at FHL (Figure 4-2). The windows of the room were covered to reduce sunlight and encourage the crabs to behave and feed normally, as *C. productus* are more likely to forage in shallower water nocturnally (Robles et al., 1989). A wooden plank was placed between the clear-walled tanks to prevent the crabs from seeing one another. Each tank contained a cinder block, a brick, and several large rocks to serve as three-dimensional habitat for the crabs (Figure 4-2).

The crabs were given a period of three weeks to acclimate to the tanks. In the first week, the crabs were fed salmon scraps to confirm their willingness to feed, but thereafter the crabs were starved until the beginning of the feeding trials.

The snails were housed in a tall-sided (~45 cm) plastic container within a separate sea table with running seawater. The hermit crabs, unable to climb the smooth plastic walls, were stored in the same sea table as the snails. The snails and the hermit crabs were not actively fed during the experiment, but did have access to small barnacles and detritus for sustenance, respectively. It also appeared that the hermit crabs cannibalized small specimens of *P. granosimanus* and *P. hirsutiusculus* with which they were housed.

Feeding trials

In each of the feeding trials, the crabs were presented with four specimens: two snails and two hermit crabs (Figure 4-3). The snails and hermit crabs were matched beforehand to create similar-sized snail-hermit crab pairs. Only the better-quality shelled hermit crabs were selected, to reduce any possible shell quality disparity between the snails and the hermit crabs. The snails' and hermit crabs' shells were measured (height, width, and thickness at aperture) and various aspects of shell quality were noted, including: degree of worm borings; shell surface erosion; green surface staining from algae; encrustation by barnacles, bryozoan colonies, or worms; any other shell damage. These data were used to match snails and hermit crabs into pairs of similar shell size and quality.

The feeding trials were conducted in the dark, using the red light of a headlamp to view the crabs' behavior, as red light is less detectable to the crabs and thus less disruptive (Cronin and Forward, 1988). The four prey specimens were placed in the front-center area of the tank. Effort was made to assure both types of prey (snail and hermit crab) were the same distance from the crab, so as not to influence the crab's initial choice.

Upon placing the prey specimens in the tank, a stopwatch was started to record the timing of crab and prey behaviors. If the crab did not attack any prey item for 30 minutes, the prey were removed and no further trials were attempted for that crab until the following day. The crab and the prey specimens were observed and all movements were recorded. Behavior was monitored until all prey were consumed, or until the crab had gone 30 minutes without attacking prey.

For Rosencrantz, 13 trials were initiated, with Rosencrantz feeding in ten of those trials. For Guildenstern, 14 trials were initiated, with Guildenstern feeding in eight of those trials. In each trial, the predatory crab had access to two snails and two hermit crabs. The order of attack and consumption were recorded to assess any preferences for certain prey. The times of attack initiation, feeding cessation, and other changes in behavior were recorded when observable; at times, the crabs were not observable due to low light, water turbidity (particularly while eating), or to the crabs being behind the three-dimensional habitat structures.

Due to the low availability of prey for the experiment, specimens that were not attacked were reused in subsequent trials. At the end of the project, the few remaining live snails and hermit crabs were returned to Argyle Creek. Both crabs were released off the FHL dock where they were caught.

Statistical Analyses

To assess overall prey preference, the numbers of the first prey chosen of each prey type (snail or hermit crab) in each trial were compared with a random distribution (the same number of snails as hermit crabs). The experimental and random prey distribution were compared using Fisher's exact test.

In addition to initial prey preference, I also tested whether the second prey items were selected randomly by the predators. In a case where the predator selects a snail as its first prey, random prey selection would mean that there is a 2/3 chance of selecting a hermit crab as the second prey (i.e., the second prey is likely to be different than the first prey). To test second-prey consistency, I noted whether the prey type was the same or different than the first selection. The experimental distribution of "same" and "different" prey were compared with a random distribution (one-third "same", two-thirds "different") using Fisher's exact test. If the experimental distribution favored the same or different prey to a significant degree, it indicated that the second prey choice was not random.

I also examined duration of the attacks and the time lapse between attacks to see if foraging and handling time varied with predator or prey identity or with order of attack. I calculated handling times for most of the attacks, measured from the time of attack initiation to the time the crab ceased crushing or eating the prey. I used the Wilcoxon Rank Sum test (aka Mann-Whitney U) to determine whether the distribution of handling times differed for several comparisons of predator identity (Rosencrantz or Guildenstern) and prey identity (hermit crab or *Nucella lamellosa*).

The Wilcoxon RS test was also used to compare handling times based on the order of the attack (first, second, third, or fourth) to determine if handling time increased or decreased through the duration of the individual feeding trials.

Lastly, I compared the time lapse between attacks (measured from the cessation of handling of the previous prey to the initiation of attack on the subsequent prey) to determine whether foraging time changed through the duration of the individual feeding trials.

RESULTS

In total, Rosencrantz attacked 14 snails and 19 hermit crabs (all prey except three hermit crabs were killed). Guildenstern attacked 13 snails and 14 hermit crabs (all prey except one hermit crab were killed). Table I summarizes the attacks by each crab.

Prey preference

The crabs did not exhibit a preference for one type of prey (Fisher's exact test, p = 0.7319, n = 17 trials). Neither crab exhibited an individual preference, either (Rosencrantz attacked 5 hermit crabs and 4 snails, p = 1, n = 9 trials; Guildenstern attacked 2 hermit crabs and 6 snails, p = 0.6084, n = 8 trials) (Table I). Note that the crabs' "preferences" were not consistent: Rosencrantz attacked more hermit crabs first, while Guildenstern attacked more snails first. There were no apparent trends in prey preference through the course of the trials (Table I).

Prey choice consistency

The crabs did exhibit some consistency in second prey choice, attacking the same prey type as their first attack more often than not (Fisher's exact test, p = 0.0366, n = 17 trials). This pattern was primarily driven by Rosencrantz, who chose the same prey 8 out of 9 times (p = 0.0498, n = 9), whereas Guildenstern selected the same prey only 5 out of 8 times (p = 0.619, n = 8).

Handling time

In the comparisons of handling times, the handling time of snail prey (both predators combined) was significantly longer than that of hermit crab prey (snail prey median = 7 minutes, hermit crab prey median = 4 minutes) (Wilcoxon Rank Sum test, $W = 146$, $p = 0.009$) (Table 4-2; Figure 4-4). There were no other significant differences among the other comparisons, but mean and median handling times were consistently longer for snail versus hermit crab prey and were consistently shorter for Rosencrantz compared with Guildenstern (Table 4-2).

Handling time did not vary based on order of attack, with no significant differences among the attack orders and no apparent trend from first to last attack (Table 4-3). There were also no significant differences in the time lapses between attacks based on attack order (Table 4-4).

Description of predator and prey behavior

Below, representative behaviors for predators and both prey are described. Note that individual behavior in a given trial may have varied, but the behaviors described are typical.

Predator: *Cancer productus*

Upon initiation of the trial (in trials where the crab did feed), the crab remained still for a short time (0-19 minutes) before slowly approaching the shells. In some cases, the crab would attempt to seize the first shell it came upon; at other times, the crab would walk over one or more shells before attempting to seize one. At times, the crab appeared to walk directly toward prey it intended to attack, while at other times the crab appeared to accidentally come upon prey while wandering the tank.

In the case of seizing snail prey, the crab merely removed the snail from the floor of the tank (the snail being adhered to the floor with its foot). The behavior of seizing hermit crabs was more deliberate: when the hermit crab was already moving about, the crab slowly approached the hermit crab, as if stalking it, before lunging toward the hermit crab, chelipeds spread, to encircle the prey. If the hermit crab fled, the lunging crab typically pursued it for several inches, either catching the hermit crab or abandoning the pursuit. This stalking behavior was not observed when crabs approached snail prey.

Because the prey were placed in the tank in close proximity to one another, the crab sometimes seized more than one shell at a time. After grabbing one shell, the crab tucked the first shell under its body, among its walking legs, before reaching for and encircling a second shell. The crab then crushed and consumed the second shell while holding the first shell.

Once the shell was seized, the shell-handling behavior of the crabs was consistent with that described by previous authors (Zipser and Vermeij, 1978; see Stafford et al. (in review) for list of additional references). Handling phases included an elbowing phase (*sensu* Zipser and Vermeij, 1978), where the crab flexed its chelipeds to shear the shell. There was a holding/pressure phase (*sensu* Zipser and Vermeij, 1978), where the crab sat ostensibly motionless, squeezing the shell, probably to induce fatigue loading fracture (Zipser and Vermeij, 1978; Miller and LaBarbera, 1995).

When handling hermit crab prey, the crabs were often observed to grasp the hermit crab by the legs, rather than the shell. This prevented the hermit crab from escaping the shell (see hermit crab behavior, below). It was not clear whether this leg-grasping behavior is a strategy to prevent the hermit crab from fleeing, or if it is simply due to an impulse to grab the moving part of the prey. I also observed leg-grasping behavior in a separate experiment, by *Hemigrapsus nudus* and juvenile *Cancer productus* attacking small *Pagurus* spp.

Prey: *Pagurus granosimanus*

The hermit crab crabs did not limit their movement or hide in the presence of the crab. They often approached when the crab was feeding on a snail, but did not approach the crabs directly when the crabs were not feeding (though at times the hermit crabs would pass close by the crabs). The hermit crabs only behaved defensively when actively pursued by the crab. This occurred either when the crab happened to stumble over a hermit crab, or when the crab lunged after a moving hermit crab, whereupon the hermit crab would flee from the crab. In at least two cases, the hermit crab escaped, but at least two other times the hermit crab began its flight too late and was caught. Twice, a hermit crab was able to survive attack by dropping out of the shell. This was never directly observed (due to the poor viewing conditions), but the surviving, naked hermit crabs were found later when the tank was cleaned of debris. During many attacks, the hermit crab was seized not by the shell but by the legs, preventing it from escaping.

Prey: *Nucella lamellosa*

It is not clear to what degree the snails altered their behavior compared to a crab-free environment, because no crab-free behavior observations were conducted. The snails' behavior appeared consistent with other accounts of defensive behaviors (Scarratt and Godin, 1992; Mima et al., 2001; Dalesman and Inchley, 2008). The snails typically did not move if the crab was nearby (within approximately 30 cm). If the crabs were far (and not actively foraging), the snails would move toward the vertical walls of the tank or nearby rocks. The snails did not move when the crabs were actively foraging. Besieged snails attempted to adhere to the bottom of the tank when the crab grappled with them. Once the crab dislodged the snail from the floor, I was unable to observe either whether the snail immediately withdrew into its shell, and whether it stayed withdrawn through the duration of the attack.

DISCUSSION

Cancer productus' foraging and feeding behavior can be divided into several stages. In each of these stages, the different prey types present differing costs and benefits.

Phase 1: Identify prey

In this study, *C. productus* appeared to forage visually, tactily, and possibly chemically. This experiment was not designed to determine the mode of prey identification, but some tentative conclusions can be drawn from the crabs' behavior. The crabs appeared to, at times, identify both prey types visually. The hermit crabs may be more susceptible to detection because they are considerably more mobile than the snails. Frequently, the crabs appeared to respond to hermit crab motion and to initiate pursuit (pursuit was recorded in at least four trials, and stalking in several more). The crabs only exhibited stalking behavior (slowly approaching the prey before lunging to grasp the prey, followed by a short pursuit if the prey was not immediately caught) when approaching hermit crabs (not when approaching snails), suggesting that the crab was capable of distinguishing between the prey types.

In cases where the prey (hermit crab or snail) was motionless, the crabs sometimes appeared to notice the prey only when they walked over the shells. The degree to which chemical identification of the prey facilitated foraging is impossible to tell without further research.

Phase 2: Catch prey

Hermit crabs' mobility is an advantage for avoiding capture, as the hermit crabs tended to flee when crabs lunged toward them in pursuit. Previous work has shown that hermit crabs are less likely to take refuge in their shell when a predator's chemical effluent is present, and instead rely on flight as a defense; this is particularly true when the hermit crabs inhabit "weak" shells, suggesting that the hermit crabs can assess their own vulnerability based on shell quality (Mima et al., 2001). Snails, on the other hand, move too slowly to actively escape the predatory crabs. Furthermore, when the hermit's shell is seized, the hermit crab is still able to escape by dropping out of the shell and fleeing, naked. Although *Nucella lamellosa* has been observed to detach from the shell (Koy, 2007), such an act would only hasten the snail's demise. Hermit crabs may be prevented from escaping, however, if the crab grasps the prey by the legs, rather than by the shell (see Phase 4).

Another consideration for prey capture is that the hermit crabs often approached when the crab was feeding on a snail. This is very likely due to hermit crabs' attraction to snail kill sites (McLean, 1973; Gilchrist, 1984; Rittschoff et al., 1990). Since the hermit crab and snail prey used in the trials were matched for shell size, the snail shells would likely have been upgrades over the hermit crabs' current shells (due to fewer interior shell bionts). The hermit crabs came within reach of the feeding crabs, and only initiated flight when the crab lunged. In cases where the hermit crab was caught by the crab, the hermit crabs' attraction to the snail kill sites was costly (and the potential benefit was nil, as the crabs almost always completely crushed the snail shells while feeding). Based on previous research, it appears that hermit crabs' attraction to snail kill sites is triggered by snail effluent, and is not related to the type of predator (McLean, 1973; Gilchrist, 1984; Rittschoff et al., 1990; Hazlett and Rittschoff, 1997). Thus, the hermit crabs may not "know" whether they will face a threat from a crab or will encounter a more benign predator, such as a drilling gastropod.

Phase 3: Crush shell

The force and time necessary to crush a shell is dependent on its strength, in turn a function of shell size, thickness, and other physical properties (LaBarbera and Merz, 1992). The shells of living snails tend to be stronger than those of hermit crabs, because hermit crabs do not maintain the shell as well as snails do (LaBarbera and Merz, 1992). A survey of a hermit crab population will generally reveal that the shells, on average, are in much poorer condition than those on live snails. Thus, the shells of live snails will typically be more difficult to crush than those inhabited by hermit crabs. Merely in terms of crushing, hermit crabs are a less-costly prey choice than live snails. In the experiment, I attempted to mitigate the effects of shell quality by selecting hermit crab and snail shells of matched size and apparent quality. The matched shells had similar degrees of exterior erosion and encrustation; however, the hermit crab shells did have epibionts on the interior shell surface that the snails did not.

I found that handling time was significantly shorter for hermit crab prey than snail prey. This may be in part due to easier shell crushing. Handling time did encompass both shell crushing and prey consumption (see Phase 4). Due to the poor visibility during observation, it was usually not possible to distinguish crushing from consumption. In fact, the crabs may alternate between phases, eating when enough flesh is accessible and crushing when better access is needed.

To better control for shell quality, it would be ideal to put the hermit crab prey into fresh shells harvested from live snails. Such an experiment would not reflect the reality of most crab-hermit crab-snail systems, where hermit crab shells are weaker than snail shells, but it would help to determine whether the shorter handling time for hermit crab prey is due to reduction of the crushing phase or reduction of the consumption phase.

Phase 4: Consume flesh

Consumption entails both the cost of accessing the edible flesh and the benefit of energy gained from the flesh. Hermit crabs may be easier to consume in that they can be removed completely from the shell, whereas snails are physically attached to the shell. In fact, if the crab is able to remove the hermit crab before the hermit crab can retract into the shell (or drop from the shell and flee), it can bypass the crushing phase completely. Snail prey, on the other hand, likely require a more extensive extraction.

The crabs were observed to grasp hermit crabs by the legs, perhaps in an attempt to remove the prey from the shell without having to break the shell. If the crab can grab the hermit crab’s legs before the hermit crab withdraws into or flees out of the shell, it may be able to pull the hermit crab out of the shell. However, the crabs crushed most of the shells they attacked, even when the hermit crab escaped before being consumed.

A critical difference between hermit crab and snail prey is the amount of edible flesh available relative to the size of the shell. The snail's body is almost entirely soft tissue. The hermit crab's body is mostly covered in hardened cuticle, except for the abdomen. During the experiment, the crabs consistently did not consume the hermit crabs' legs or carapace. This avoidance of, or inability to process the hermit crabs' hard parts was also observed when a juvenile *C. productus* was fed much smaller *P. granosimanus* specimens (Stafford, unpubl. data). In one instance, the juvenile crab was observed holding the extracted hermit crab by the carapace with both chelae while picking at the abdomen with its mouthparts. It is reasonable to suspect that the adult crabs fed on hermit crabs in a similar way. Both the juvenile and adult crabs were also observed tearing the hermit crabs' legs from the carapace, though it was impossible to tell whether this was to disable the prey or to facilitate feeding.

Because the crabs consumed much less edible flesh from the hermit crabs than the snails, this may contribute to the shorter handling time of hermit crab prey, but also reduced the potential energy profit. As stated above, further experiments would be needed to determine the relative contributions of shell crushing and flesh consumption to total handling time.

Consequences for crab-snail-hermit crab systems

The overall balance of costs and benefits, combined with the observations in this experiment, do not implicate a certain preferred prey. In terms of handling costs, snail prey appear to require more time and strength to crush, but they presumably may offer a greater energy benefit. The ultimate profitability of each prey is still uncertain, and warrants further research.

A major consideration for natural systems that was not tested in this experiment was prey encounter rate. With two of each prey item available in a small (90 cm by 120 cm) enclosure, the crabs' hermit crab:snail encounter ratio was likely random. The hermit crabs, due to their mobile nature, may have been more conspicuous to the crabs (Rossi and Parisi, 1973), but any effect from this conspicuousness was not enough to result in an apparent preference for hermit crab prey.

The crabs' first-prey choice was random, suggesting that the crabs neither actively sought out one prey type nor happened to encounter one prey type more frequently. In fact, the crabs' behavior may indicate that they are patch-foragers, seeking aggregations of prey and then attempting to consume all the prey available in the patch (Stephens and Krebs, 1986). This is one potential explanation for the fact that the crabs tended to consume the same prey type in the first two attacks (Table 4-1). Due to the behaviors of each prey type, the two individuals of each type were often near one another. The snails, being placed near one another at the initiation of the trial, stayed near one another if they did not move from their original places (especially if the crab was actively foraging). The hermit crabs are more mobile, but are also quite gregarious, and tended to move about the tank with one another. Thus, when a crab encountered one prey type, it was likely that the second individual of this type was nearby. The crabs commonly grabbed more than one shell at a time, holding a second or even third shell with their walking legs while they crushed the first shell with their chelae. Such patch-foraging would be consistent with observations made by myself and others during an experiment where *C. productus* were allowed to forage among patches of *Mytilus trossulus* mussels (unpubl. data). The crabs grabbed an entire patch of mussels, and crushed them indiscriminately, rather than hunting and capturing one shell at a time. The crab then abandoned the patch when most of the shells had been crushed and at least partially consumed, even if not all the edible flesh had been eaten. Similarly, in the present study, the crabs were "messy eaters", often crushing a prey but then leaving a significant amount of edible flesh behind (particularly with *N. lamellosa* prey). This may suggest that at a certain point, continuing with the current patch is no longer profitable, so the crab will abandon the patch and seek new patches. Further experiments, controlling the prey composition of prey patches, may confirm this patch-foraging behavior.

A related explanation for the consistent first-two-prey choice may be that the crabs tend to hone in on whatever prey type they happen to attack first. Since both *N. lamellosa* and *P. granosimanus* exhibit patchy, gregarious distributions, it is likely that a single prey of either type will be near other prey of that type. If the crab can focus on the characteristics of that first prey, it may be more likely to find and capture additional prey. Further experiments exploring sequential prey choice, where the effects of prey patchiness are eliminated, may show whether first-prey identity truly influences second-prey choice.

Based on the crabs' stalking behavior, it appeared they were able to distinguish between the hermit crab prey and the snail prey. While is it possible that the crabs were familiar with each prey type individually, it is also possible that crabs have different attack strategies for mobile versus non-mobile prey. It may be enlightening to perform an experiment using prey with a range of mobilities (for instance: sessile mussels, sedentary clams, sporadically swimming scallops, and highly mobile small crabs such as *Hemigrapsus* spp.) to determine whether *C. productus* attack behaviors are prey-specific.

The present study addresses a limited system: that of *C. productus* and two of the hermit crab and snail species with which it coexists in the Northeastern Pacific. This will be, hopefully, only one among many case studies to examine the behavior and prey preference of the major crushing predators of gastropod shells around the world. More importantly, though, this study opens many potential courses of inquiry. In the experiment, the strongest finding was that handling time is significantly shorter for hermit crab prey than for snail prey. Is this discrepancy due to differences in crushing time or flesh consumption? Does this discrepancy hold true outside of the laboratory setting? I also found no preference for hermit crab prey over snail prey, despite this difference in handling time. Is this due to the greater amount of edible flesh yielded by snails? Or do crabs select prey based on patches, only specializing their attack technique (e.g., stalking hermit crab prey) once prey characteristics are ascertained?

CONCLUSIONS

Predatory *Cancer productus* exhibit longer handling times when attacking and consuming snail prey over hermit crab prey. This may be because hermit crabs have weaker shells and possess less edible tissue than live snails. Although *C. productus* exhibited no preference for either snail or hermit crab prey, second-prey-choice (per trial) tended to be the same as first prey choice. Further research may determine whether this is a result of crab foraging behavior or an experimental artifact.

FIGURES

Figure 4-1. Two live *Nucella lamellosa* (Gmelin, 1791), exhibiting bioerosion and encrustation. The left specimen, with its aperture badly damaged, was not used in the predation trials.

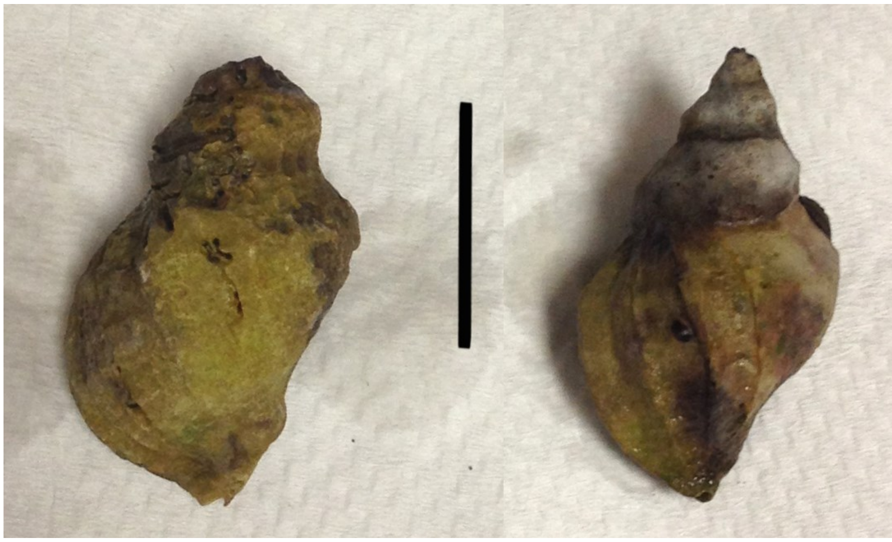


Figure 4-2. Left: Schematic of one 90 cm by 120 cm sea table, with rocks and bricks for 3D-habitat complexity. Right: Crab in empty sea table, before habitat and water.

Figure 4-3. Apertural (L) and abapertural (R) views of four prey specimens chosen for a single predation trial. The top two specimens are one snail and one hermit crab, matched for shell size and quality. The bottom two specimens are also one snail and one hermit crab, matched for shell size and quality. Scale bars represent 2 cm.

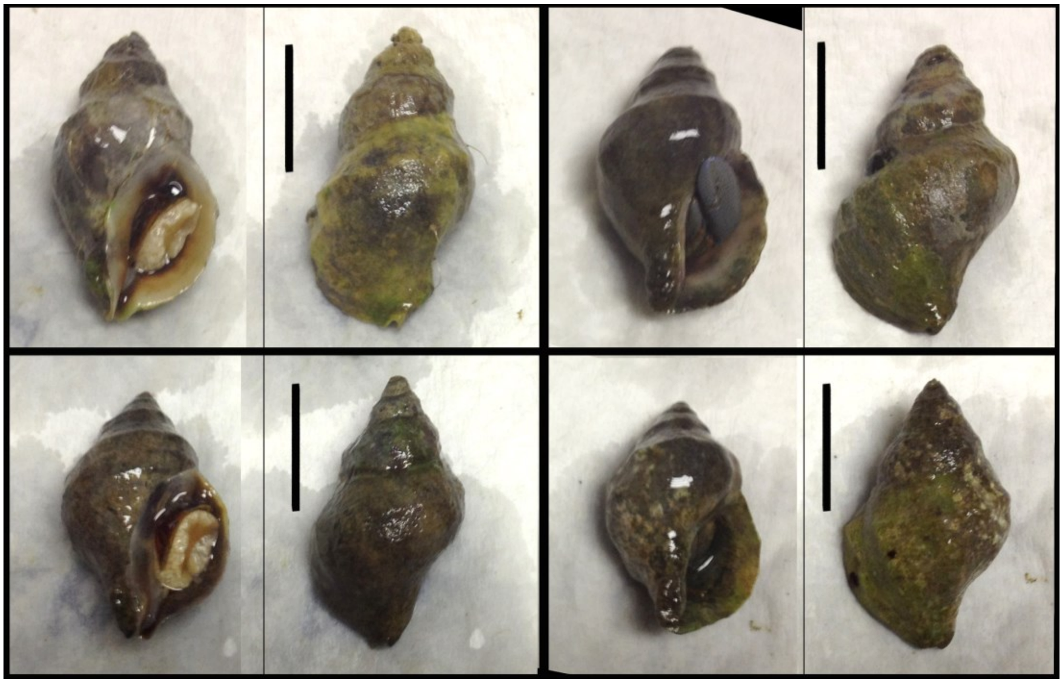
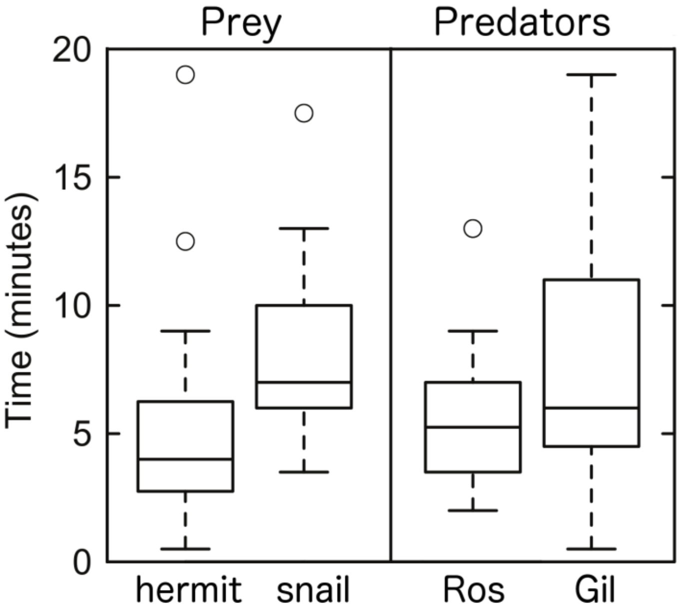


Figure 4-4. Box plots showing the distribution of handling times (in seconds). Left: Handling times of hermit crab prey versus snail prey. The distributions were significantly different (Wilcoxon Rank Sum test, W = 146, p = 0.009). Right: Handling times of each crab predator (Rosencrantz versus Guildenstern). The distributions were not significantly different.

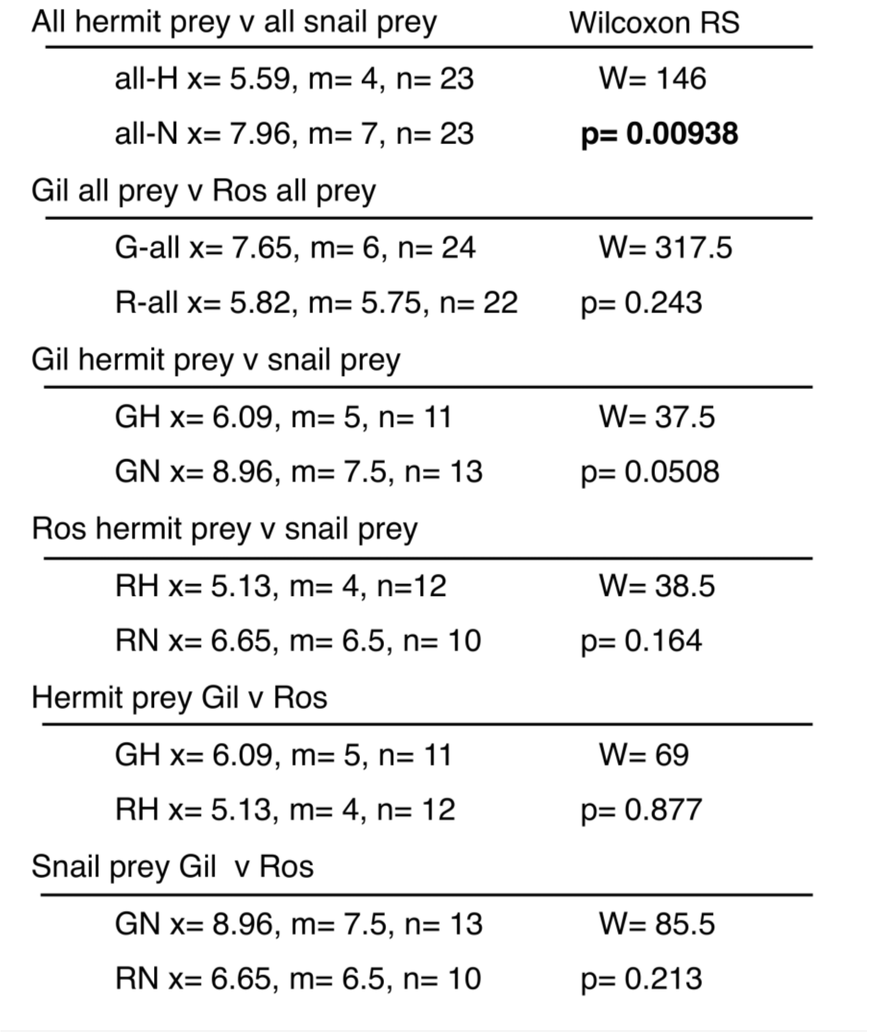


TABLES

Table 4-1. The prey identities and order of attacks for each trial for each predator. H: hermit crab prey attacked, S: snail prey attacked. Zeros indicate that no prey was attacked (the crab either ceased foraging or never initiated foraging in a given trial). In three trials, the experiment was conducted with only one predator (N/A = no prey were offered to the second predator). In Rosencrantz Trial 14, the crab grabbed both a hermit crab and a snail at the same time, and it was impossible to determine which prey was chosen first.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Rosencrantz															
1st	H	S	S	S	S	H	H	H	0	0	0	N/A	H	H/S	N/A
2nd	H	H	S	S	S	H	H	H	0	0	0		H	H/S	
3rd	S	S	H	H	H	0	S	0	0	0	0		S	S	
4th	S	H	H	H	H	0	0	0	0	0	0		0	0	
Guildenstern															
1st	S	S	S	H	0	N/A	S	0	0	0	S	H	H	0	0
2nd	S	S	H	S	0		S	0	0	0	S	S	H	0	0
3rd	H	H	H	H	0		H	0	0	0	H	S	0	0	0
4th	H	H	S	0	0		H	0	0	0	H	H	0	0	0

Table 4-2. Handling time comparisons based on crab predator identity (Rosencrantz and Guildenstern) and prey identity (hermit crabs versus snails). x = mean handling time (seconds); m = median handling time (seconds); n = number of attacks included in analysis; W = Wilcoxon rank sum.



All hermit prey v all snail prey	Wilcoxon RS
all-H x= 5.59, m= 4, n= 23	W= 146
all-N x= 7.96, m= 7, n= 23	**p= 0.00938**
Gil all prey v Ros all prey	
G-all x= 7.65, m= 6, n= 24	W= 317.5
R-all x= 5.82, m= 5.75, n= 22	p= 0.243
Gil hermit prey v snail prey	
GH x= 6.09, m= 5, n= 11	W= 37.5
GN x= 8.96, m= 7.5, n= 13	p= 0.0508
Ros hermit prey v snail prey	
RH x= 5.13, m= 4, n=12	W= 38.5
RN x= 6.65, m= 6.5, n= 10	p= 0.164
Hermit prey Gil v Ros	
GH x= 6.09, m= 5, n= 11	W= 69
RH x= 5.13, m= 4, n= 12	p= 0.877
Snail prey Gil v Ros	
GN x= 8.96, m= 7.5, n= 13	W= 85.5
RN x= 6.65, m= 6.5, n= 10	p= 0.213

Table 4-3. Comparisons of handling time based on order of attack. Top: Wilcoxon rank sums and p-values (no significant differences). Bottom: mean and median handling times (in seconds) for first, second, third, and fourth attacks (n = number of attacks included).

	First	Second	Third
Fourth	W = 51.5 p = 0.446	W = 68.5 p = 0.273	W = 63 p = 0.176
Third	W = 68 p = 0.604	W = 83 p = 0.516	
Second	W = 92.5 p = 0.922		

	Mean	Median	n
First	7	6	12
Second	6.23	6	15
Third	7.5	6.5	13
Fourth	5.21	4	7

Table 4-4. Comparisons of time lapses between attacks (measured from the cessation of the previous attack to the initiation of the following attack) using Wilcoxon rank sums. "2-1" is the time lapse between the first and second attacks; "3-2", between the second and third attacks; "4-3", between the third and fourth attacks. Numbers reported: x: average time lapse in seconds; m: median time lapse in seconds; n: number of lapses measured; W: Wilcoxon rank sum.

2-1 v 3-2	Wilcoxon RS
2-1: x = 2.83, m = 1, n = 12	W= 86.5
3-2: x = 5.71, m = 1.25, n = 14	p= 0.620
3-2 v 4-3	
3-2: x = 5.71, m = 1.25, n = 14	W= 56
4-3: x = 6.50, m = 4.5, n = 7	p= 0.817
2-1 v 4-3	
2-1: x = 2.83, m = 1, n = 12	W= 41.5
4-3: x = 6.50, m = 4.5, n = 7	p= 0.456

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CHAPTER 5

A FOSSIL APPLICATION OF VERMEIJ CRUSHING ANALYSIS AND COMPARISONS WITH MODERN GASTROPOD ASSEMBLAGES FROM THE PACIFIC NORTHWEST OF NORTH AMERICA[3]

INTRODUCTION

Vermeij Crushing Analysis (VCA), modified from a method developed by Vermeij (1982), estimates the occurrence of crushing predation on assemblages of shelled organisms. In a previous paper (Stafford and Leighton, 2011), we used VCA to examine taphonomic and predation patterns on four species of nearshore marine gastropods from Torrey Pines State Beach in southern California. Utilizing a modern assemblage of *Olivella biplicata* (Figure 5-1a) from Bamfield, British Columbia, our present paper addresses further issues regarding the use of VCA, including the consistency of results among multiple repetitions, the impact of sample size on the reliability of results, and the potentially confounding influence of hermit crab habitation on the interpretation of predation on gastropods. In addition to addressing these logistical and interpretive aspects of VCA, we compare the results of the Bamfield assemblage to the previous results from the Torrey Pines conspecifics. Lastly, we apply VCA to an assemblage of *Bulliopsis marylandica* (Figure 5-1b) from the Miocene St. Mary's Formation of Maryland. *Bulliopsis* and *Olivella* share much in terms of shell morphology, habitat and feeding ecology, and predatory environment. VCA may show whether these similarities are borne out in crushing predation patterns.

Vermeij Crushing Analysis establishes a baseline taphonomic damage profile for an assemblage of shelled organisms, typically gastropods or bivalves, by measuring the frequency of damage on those shells bearing complete naticid drillholes; such drillholes indicate that these animals were most likely killed by drilling predators, and thus any additional fragmentary damage occurred post-mortem and is unrelated to crushing predation (Vermeij, 1982). At the same time, damage frequencies are measured on the undrilled shells, for which the cause of death is unknown (some prey may have been killed by crushing predators). A statistical test is used to determine whether the damage frequencies differ between the drilled and undrilled

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[3] A version of this chapter has been submitted for publication. Stafford and Leighton, *Palaeogeography, Palaeoclimatology, Palaeoecology*

portions of the assemblage. Then, the drilled-damage frequencies are subtracted from the undrilled-damage frequencies. In most cases, the difference is positive, i.e., the undrilled shells have higher damage frequencies than the drilled shells. This difference represents damage due to crushing predation (see Methods for a more detailed description of the VCA protocol).

The purpose of VCA is to solve several problems associated with the investigation of crushing predation on shelled prey. A general issue with studying predation is that it is difficult to observe predatory events *in situ*, and such observations, when accomplished, cannot necessarily be extrapolated to draw conclusions about population-level ecological and evolutionary consequences. To understand the influence of predation on evolutionary scales, large sample sizes are required to ensure representative results. VCA, like many other proxies for predation (e.g., repair scar frequency, predatory drilling frequency), draws information from a large assemblage of shell specimens, rather than relying on the observation of individual predatory events (Stafford and Leighton, 2011). Thus, the results are applicable at the population scale and can be used to explain or predict ecological and evolutionary patterns in predation. Furthermore, since VCA relies on assemblages of dead shells, rather than the observation of live populations, it can potentially be used in both modern and fossil contexts to examine predation both over space and through time.

An issue with studying crushing predation, in particular, is that much of the evidence of predatory interactions is destroyed in the interaction. Crushing predators, by nature, tend to fragment shells into multiple pieces; these pieces may be difficult to distinguish from non-predatory, taphonomic damage. VCA enables one to distinguish taphonomic damage from predatory damage on the whole-assemblage level, making it less critical to distinguish specific instances of predatory damage from taphonomically induced damage on individual shell specimens.

Lastly, VCA addresses a limitation of a common predation variable, shell repair scar frequency. Repair scars represent healed shell damage from a failed predatory attack. While repairs are relatively easy to identify, the proper interpretation of repair frequency results is ambiguous: because repair scars represent failed predatory attacks, the relationship between repair frequency and predatory mortality (the proportion of the prey population that dies due to predation) may be unclear (Vermeij, 1987; Leighton, 2002; Alexander and Dietl, 2003). VCA has the advantage of approaching prey mortality more directly, through dead shells. Furthermore, VCA can be used with populations of gastropods in which repair scars are difficult to assess; with *O. biplicata*, the smooth, unornamented shell does not show repairs well. Unrepaired predatory fragmentation is easy to recognize, as long as it can be distinguished from taphonomic damage, making VCA a practical alternative or complementary method to repair frequency.

Mondal et al. (2014) found that the best information about predation was obtained by using VCA-like data on crushing predation in conjunction with repair scar data, since each metric captures a different component of the predatory system. Repairs were only infrequently observed on the two study taxa, *O. biplicata* and *B. marylandica*, so it was not possible to analyze both VCA and repair data in the present study. Our present examination of VCA seeks to establish a valid and consistent protocol for VCA to be used with repair frequency and other predation metrics in assemblages where such metrics are available.

In this study, we use VCA to examine crushing predation in two gastropod assemblages, one modern and one fossil. The fossil taxon, *B. marylandica,* is morphologically and ecologically similar to the *O. biplicata* examined in the present paper and previously (Stafford and Leighton, 2011). We assess the potential for VCA to assess crushing predation in fossil assemblages, and compare the *B. marylandica* results to those of modern *O. biplicata* from both Bamfield and Torrey Pines.

To best approach the above practical applications, the current study first explores several logistical and interpretive issues critical to the use of VCA. While these issues were touched upon in our previous study (Stafford and Leighton, 2011), they warrant a deeper look. Any method that seeks to draw conclusions about entire populations of organisms depends on a sufficient sample size to yield accurate results. In this study, we examine the effect of sample size (particularly small sample size) on the significance and reliability of VCA results. Depending on the abundance, preservation, and drilling frequency of gastropod specimens in a given assemblage, it may be difficult to obtain large sample sizes of both drilled and undrilled shells. It is useful to know the lower limit on sample size that still permits application of VCA.

A second issue we examine in this study is the consistency of damage identification on the drilled shell assemblages. The first step of VCA is to identify the damage on individual shells. Presence-absence data are produced for each damage category, but some of the categories represent segments of a continuum. While each segment of the continuum has a discrete definition, in reality the assignment of damage to one segment or another is somewhat subjective and prone to human error. For VCA to be applicable, it must be replicable. To test the consistency of damage identification, the damage inventory was repeated multiple times for a single subsample of the shell assemblage and the resulting damage frequencies were compared. We also present a simplified protocol for VCA, based on biologically meaningful categories, that yields similar results to the original protocol, while reducing both the time investment required for data collection and the influence of subjectivity.

A third issue, explored to a limited degree in the previous study (Stafford and Leighton, 2011), is the effects of hermit crab habitation on the accuracy and interpretation of VCA. Hermit crabs inhabit gastropods after the death of the original gastropod. On individual shells, it may be impossible to tell whether predatory fragmentation was incurred by the original gastropod or a later hermit crab. If hermit crabs expressed no preference among drilled and undrilled shells, such hermit crab predation damage would be accounted for in the taphonomic profile. However, researchers have shown that hermit crabs tend to prefer undrilled shells (Pechenik and Lewis, 2000; Pechenik et al., 2001). If, in a given assemblage, hermit crabs did inhabit undrilled shells preferentially, any predation damage incurred on these hermit crabs would *not* be picked up in the taphonomic profile, and may be misinterpreted as predatory damage in the original gastropod population. Fortunately, certain types of shell damage are indicative of hermit crab habitation (Walker, 1989). In our previous study (Stafford and Leighton, 2011), we performed a rudimentary correction for hermit crab habitation utilizing these hermit crab-associated damage categories. In this paper, we refine the hermit crab correction to reduce the effect of hermit crab habitation on the VCA results.

As the application of VCA to real assemblages is dependent on development of a consistent and robust protocol, the logistical examination of VCA will be presented first, as an independent set of Methods, Results, and Discussion. Second, we present the practical application of VCA on the Bamfield and St. Mary’s assemblages, along with an analysis of hermit crab habitation in the assemblages.

MATERIALS AND METHODS I

Olivella biplicata from Bamfield, BC

An assemblage of 1,067 empty *Olivella biplicata* shells (Fig. 5-1) was collected from Brady’s Beach in Bamfield, British Columbia (48.8303° N, 125.1375° W) (Fig. 5-2a). This assemblage consisted of four separate collections, one obtained in July 2009, and the other three obtained throughout July and August 2010. The shells were surface-collected during low tide from lag deposits along a 0.5-km strip of sandy beach. Shells were collected exhaustively, with no preference for intact, damaged, or drilled shells.

O. biplicata is a semi-infaunal, predatory gastropod of moderate size, between 10mm and 40mm at Brady's Beach. The Brady's Beach specimens tend to be somewhat larger than those collected in Stafford and Leighton (2011), from Torrey Pines State Beach in Southern California.

The Bamfield assemblages were used to compare simplified approaches to VCA, to check the consistency of VCA results, and to examine the effects of sample size on VCA results. Then, the Bamfield assemblages were compared to assemblages from southern California and a fossil assemblage from the Miocene of Maryland (see Methods II, Results II, and Discussion II).

Vermeij Crushing Analysis damage categories

The VCA protocol presented here is a refinement of the protocol presented in Stafford and Leighton (2011). VCA uses gastropod shell assemblages that contain both undrilled and naticid-drilled shells. Drilled shells bear a distinctive (and complete) beveled naticid drillhole, indicating that the original gastropod inhabitant was most likely killed by a naticid predator. Each shell is assessed as drilled, undrilled, or unknown. On *Olivella biplicata*, naticid drillhole location is strongly stereotyped, almost always occurring on the apertural (ventral) surface of the shell, close to the aperture and roughly centered between the apex and the siphonal notch (Fig. 5-1a). In the case of shells where this stereotypic region of the shell is missing, the shell is not included in the analysis.

In previous work (Stafford and Leighton, 2011), a set of damage categories was established representing common and identifiable types of damage found on gastropod shells. These same tested categories are applied in the present study, as they have been found to reasonably capture predation damage and taphonomic damage in the shell assemblages.

In VCA, each shell is assessed for each damage category; if it was impossible to determine whether damage was present, the shell was not included in the count for that particular damage category. Nine potentially predatory categories were assessed for each shell (Fig. 5-1c-j):

Apex abrasion: A visibly abraded apex, including abrasion resulting in a small hole in the tip of the apex.

Apex removal: All or a portion of the apex missing (Fig. 5-1c).

Aperture abrasion: Visible abrasion to outer aperture lip, including damage that extends up to 5° into the aperture (Fig. 5-1d). Where more extreme aperture damage is present, the shell is not included in this count.

5°-10° aperture damage: Material removed from the outer aperture, extending at least 5° but not more than 10° into the aperture (Fig. 5-1e). Where damage deeper than 10° is present, the shell is not included in this count.

10°-90° aperture damage: Material removed from the outer aperture, extending at least 10° but not more than 90° into the aperture (Figure 5-1f). Where damage deeper than 90° is present, the shell is not included in this count.

90°-180° aperture damage: Material removed from the outer aperture, extending at least 90° but not more than 180° into the aperture (Figure 5-1g). Where damage deeper than 180° was present, the shell is not included in this count.

>180° aperture damage: Material removed from the outer aperture, extending at least 180° into the aperture (Figure 5-1h).

Columella damage: Removal of the abapical (siphonal) portion of the columella (Figure 5-1j).

Hole in body whorl: Any hole in the body whorl not connected to aperture damage. Where a major portion of the body whorl (>180°) is missing, the presence or absence of a hole in the body whorl cannot be determined and the shell is not included in this count.

The current protocol differs from that of Stafford and Leighton (2011) in that the aperture-damage categories here are assessed exclusively; i.e., shells bearing a given category of aperture damage are excluded from the counts for less-extreme aperture damage. Previously, these categories were assessed inclusively; for a shell bearing a given category of aperture damage, less-severe damage was also marked as present. The previous protocol potentially inflated damage frequencies, whereas the present protocol is conservative.

Additionally, three hermit crab-associated categories were assessed. These categories represent damage that may indicate hermit crab habitation, and clearly are not caused by crushing predation (Fig. 5-1f, k):

Boring trails: Shell borings that are multiple and/or non-perpendicular to the shell surface (i.e., not predatory) (Fig. 5-1k).

Helicotaphrichnus commensalis boring: This trace fossil is a boring on the columella created by a spionid worm that lives in hermit crab-inhabited shells (Kern et al., 1974). When the abapical (siphonal) portion of the columella is missing, the shell is not included in this count (Fig. 5-1f).

Pinhole borings: Tiny, straight-walled borings perpendicular to the shell surface. Although these borings are categorized as hermit crab-associated, some may be due to drilling predation by muricid gastropods or octopods.

The resulting dataset is sorted according to the drilled-undrilled status of the shells. The numbers of damaged and undamaged specimens are tabulated for each damage category.

Correction for hermit crab habitation

Hermit crab habitation exposes shells to additional taphonomic and predatory damage after the death of the original snail inhabitant (Walker, 1989). On a shell that has been inhabited by a hermit crab, it may be impossible to tell if predatory damage was incurred on the snail or the hermit crab. While it is difficult to rule out the possibility of hermit crab habitation on any given shell, there are many types of damage on shells that positively indicate hermit crab habitation (Walker, 1989). By eliminating shells with hermit crab-associated damage, the potential confounding influence of predation and taphonomy on hermit crab-inhabited shells is reduced. Additionally, separating pagurized shells from the rest of the assemblage allows testing of the hypothesis that hermit crab habitation is increasing the damage frequencies of the overall assemblage. For the purposes of this study, pagurized shells were defined as undrilled shells bearing boring trails, *H. commensalis* borings, or pinhole borings. Other potentially hermit crab-related damage, such as marks left by bryozoan colonies, or abraded surfaces caused by shell-dragging, were more difficult to reliably identify and were not included.

To reduce the effect of hermit crab habitation on the assemblage, all pagurized shells (shells bearing boring trails, *H. commensalis* borings, or pinhole borings) are removed from the undrilled portion of the assemblage. Pagurized shells are not removed from the drilled portion of the assemblage. Pagurization was very rare among these drilled shells, so the effect of hermit crabs was likely minimal on the drilled assemblage. Furthermore, fragmentation on the drilled shells is known to be post-mortem, regardless of whether a hermit crab ever inhabited the shell.

Identification of damage categories likely associated with crushing predation

For both the drilled and undrilled (non-pagurized) groups, the numbers of damaged and undamaged shells are totaled for each damage category.

To determine whether the distribution of damaged-versus-undamaged shells differs between the drilled and undrilled groups, Fisher's exact test is performed for each damage category, with a p-value threshold of 0.05 chosen to determine statistical significance.

Damage frequencies, where DF = (damaged shells)/(total assessed shells), are also calculated for each category for drilled and undrilled shells. For drilled shells (whose cause of death is known: naticid drilling predation), these damage frequencies represent taphonomic damage. The taphonomic damage frequencies are subtracted from the damage frequencies of the undrilled shells. If a category of damage is more frequent in the undrilled group than the drilled group, it is likely that this additional damage is due to crushing predation. The predatory frequency (PF) is the difference between the undrilled frequency and the drilled frequency ($DF_{undrilled} - DF_{drilled}$).

A low Fisher's p-value (indicating significance) and a positive PF indicate that some degree of damage is due to crushing predation. The evidence for a crushing origin of a damage category is particularly strong in cases where the damage is extremely infrequent or absent among drilled shells (i.e., the damage is rarely or never caused by taphonomic forces).

Estimated Minimum Crushing Mortality

After identifying the categories of damage attributable to predation, the frequencies of such damage can be used to estimate the proportion of individuals killed by crushing predators. This is deemed the Estimated Minimum Crushing Mortality (EMCM). EMCM is a low-end estimate because it includes only crushing victims whose shells were well-preserved enough to persist in the assemblage; crushing predation can result in the full fragmentation and destruction of the shell, so many crushed individuals are lost to the record.

Based on the types of shell damage that have been identified as predatory in previous work (Stafford and Leighton, 2011; Stafford et al. (in review) and references therein), EMCM is determined by first back-calculating the number of individuals bearing damage attributable to predation. One method of doing this is to use the aperture damage categories. Because the aperture damage categories are exclusive (damaged specimens cannot be counted in more than one category), their data can be combined to yield a more accurate estimate than merely choosing the category with the greatest PF, as was done in Stafford and Leighton (2011). A second potential method of estimating EMCM is to use the non-aperture damage category with the greatest PF (e.g., columella damage), if the PF of this damage category is greater than the frequency calculated using the aperture damage categories.

The predatory frequency of each aperture damage category is determined and the PF is multiplied by the number of undrilled shells. Next, the number of undrilled shells bearing predatory damage is divided by the total number of shells (drilled plus undrilled). This yields an estimate of crushing mortality for the entire assemblage. However, this number can be strongly influenced by the frequency of drilling predation, so it is also useful to calculate EMCM using only undrilled shells in the denominator; this calculation gives an estimate of crushing mortality for individuals not killed by naticid gastropods.

Simplified VCA

The thorough inventory of damage categories undertaken in VCA requires a considerable time investment, as dozens to hundreds of shells are examined individually within a single assemblage. Furthermore, by recording multiple damage categories, the likelihood of producing falsely significant differences is increased relative to an examination of fewer categories. Most importantly, the value in VCA is in its ability not only to estimate crushing predation, but also to discern what types of damage are predatory and thus worthy of further study. Stafford and Leighton (2011) determined that damage greater than 90° could confidently be ascribed to crushing predation for *O. biplicata* from southern California.

We used the Bamfield, BC *Olivella biplicata* to evaluate simplified strategies for assessing predatory damage. The original aperture damage categories (aperture abrasion <5°; 5°-10°; 10°-90°; and >90°) were combined in several different ways to see which method produced results most reflective of the original inventory. In all cases, aperture abrasion <5° was eliminated, as the category is overwhelmingly attributable to taphonomy.

A. Single category: all aperture damage >5°. All aperture damage more extensive than 5° was considered as a single category.

B. Single category: all aperture damage >10°. All damage more extensive than 10° was considered as a single category, while damage <10° was ignored.

C. Two categories: damage >90°, compared with damage 5-90°. The two more extensive damage categories were combined, as were the two less extensive categories. This lumping system reflects the conclusions of Stafford and Leighton (2011) that damage greater than 90° could be attributed almost exclusively to predation within the *O. biplicata* assemblage.

The resulting damage frequencies for the three lumping strategies, as well as Fisher's exact test results between the undrilled and drilled groups, were examined to see which combination, if any, most successfully captured predatory damage while distinguishing it from taphonomic damage.

Consistency and Sample Size

Consistency of damage assessment

A subsample of 55 shells was selected randomly from the Bamfield *O. biplicata* assemblage to assess the consistency of the identification of categories on the shell assemblage. Within approximately six months of the initial damage inventory, these 55 shells were re-inventoried two times, making a total of three iterations ("1", "2", and "3"). These three iterations consisted of damaged-undamaged totals for the twelve original (uncombined) damage categories described above, plus a predatory drilling category. Drilled and undrilled shells were not separated for this analysis.

The damage totals for each iteration were compared pairwise to one another using Fisher's exact test. These comparisons were repeated for each damage category. Low p-values ($p\text{-value} < 0.05$) suggest that the damage assessments were *not consistent* between the two compared iterations. In the case of higher (non-significant) p-values, further analysis was required to rule out low sample size as the cause of the high p-values.

A potential issue created by the small sample sizes is that goodness of fit tests, including Fisher's exact test, are scale-dependent, and it is increasingly difficult to refute the null hypothesis with decreasing sample size (see *effect of sample size on statistical significance*, below). Such small sample sizes may require extreme differences to yield significant results: thus, with a sample size of 50, Fisher's exact test is less likely to detect differences that may be significant at larger sample sizes with the same proportions.

In the damage-assessment-consistency analysis described above (sample size of 55), non-significant p-values may be produced merely as a result of low sample size. An appearance of consistency among the collections may be an artifact. To remove the bias of low sample size, we artificially enlarged the sample sizes of each collection to find whether significant differences (inconsistencies among the collections) might be discovered. The damage-undamaged totals of each collection were multiplied by 10 to simulate a sample size of 550 shells. This multiplication increased the sample size but maintained the relative damage frequencies produced in the initial subsampling, resulting in a more conservative evaluation of consistency.

The increased sample size causes p-values to decrease. Significant p-values indicate that the subsampled iterations are *not consistent* with one another. Higher (non-significant) p-values indicate that the iterations are consistent, even at larger sample sizes. Thus, the categories with the lowest p-values (indicating more statistically distinguishable iterations) were deemed to be *less consistent* than those that yielded nonsignificant differences. Categories with high p-values, even after sample size inflation, were deemed to be consistent; i.e., such damage is identified sufficiently faithfully among multiple repetitions.

Effect of sample size on statistical significance

As stated above, small sample size can have a strong effect on statistical results. The Fisher's exact test, used to compare drilled-undrilled damage frequencies within damage categories, is sensitive to sample size: smaller sample sizes are more likely to yield non-significant results. Because this test is integral to VCA, in that it is used to determine whether undrilled shells bear more damage than is taphonomically predicted by drilled shells, it is important to be aware of how sample size influences the p-values produced in the test. Sample sizes must be large enough to yield significant results in cases where damage is clearly more frequent among one group of shells.

We produced model datasets to examine the interplay between sample size and the magnitude of the difference between drilled and undrilled damage frequencies. The most extreme difference between drilled and undrilled would be a case where the undrilled all bear a type of damage, while none of the drilled bear that damage. The least extreme difference would be a case where the damage frequencies were identical for both drilled and undrilled shells.

We established five sample-size levels, where sample size equals the total number of shells for a given sample. The five levels were 10, 20, 50, 100, and 1000. At each level, the damage frequencies of two hypothetical samples, A and B, were varied to reflect more-similar and less-similar frequencies.

The damage frequencies were varied in two ways. First, the frequency of sample A was maintained at 0, while the frequency of B was increased from 0 to 1.0 (100%). This is referred to as the Versus Zero method.

Second, the frequencies of A and B were varied as the inverse of one another. For a sample size of 10, if A has one damaged specimen, B has 9 damaged specimens (A = 10%, B = 90%). If A has 3 damaged specimens, B has 7 (A = 30%, B = 70%). This is referred to as the Inverse Frequency method.

When samples A and B are too similar, Fisher's exact test will yield a nonsignificant p-value. As the difference between the samples increases, there will be a difference threshold where the p-value crosses from nonsignificant to significant (in this case, p-value = 0.05). Both the Versus Zero and Inverse Frequency methods were used to determine how distinct samples A and B must be to yield a significant p-value (alpha = 0.05).

These comparisons were repeated at each sample-size level to determine the effect of sample size on the difference threshold. This, in turn, helps to discern the minimum necessary sample size for successful use of VCA.

RESULTS I

Simplified VCA

Three lumping strategies were implemented with the Bamfield *O. biplicata* dataset: all aperture damage >5°; all aperture damage >10°; and aperture damage 5°-90° versus >90°. Undrilled damage frequencies were significantly greater for all strategies except 5-90° (Table 5-1).

The greatest difference in frequency between the drilled and undrilled groups, as well as the lowest p-value, was for the strategy using the >10° category. The frequency for >10° among drilled shells was 0.11, indicating that a portion of such damage was attributable to taphonomy. The frequency of damage >90° among drilled shells was 0.02 (Fig. 5-3) suggesting that such damage was only very rarely taphonomic in origin. Its less-severe companion category, 5°-90°, did not differ significantly between drilled and undrilled shells (Figure 5-5).

Consistency and Sample Size

Consistency of damage assessment

In a consistency analysis using a subsample of 55 specimens, there were no significant differences among pairwise comparisons of the three iterations for each damage category (Table 5-2). Because the results of the Fisher's exact test are sensitive to sample size, the pairwise comparisons were performed again after multiplying the damage occurrences by ten to simulate a sample size of 550 shells. With the differences between the three iterations propagated through this larger sample size, significant differences appeared in five categories: only one of these categories (columella damage) is associated with predation based on VCA (Table 5-2). Each of the remaining categories, including the potentially predatory aperture damage categories, was consistent among the three iterations, despite the enlarged sample size.

Effect of sample size on statistical significance

The frequency difference thresholds were determined for each sample-size level (10, 20, 50, 100, and 1000) (Table 5-3). With increasing sample size, the threshold differences become narrower: At n = 10, 0% is distinguishable from 50% and 20% is distinguishable from 80%. At n = 1000, 0% is distinguishable from 0.6% and 47.7% is distinguishable from 52.3%. Narrower differences are not statistically different.

DISCUSSION I

Simplified VCA protocol

Because crushing predation can produce many different types of damage, no single damage category can fully capture the total amount of damage due to crushing predation; i.e., the frequency of any particular damage category attributable to predation is an underestimate of the actual frequency of the total crushing predation in the assemblage. For simplified VCA, the goal is to find a category (or combination of categories) that A) maximizes the frequency of damage attributable to crushing predation (to get as close to the "real" crushing frequency as possible) and B) can be applied consistently and easily for the comparison of many assemblages. Among the combined categories we tested, the greatest difference in frequency between the drilled and undrilled groups was for the >10° strategy (Figure 5-5). The >5° strategy, with an undrilled frequency of over 0.9, was still mostly attributable to taphonomy (over 0.7). The >90° strategy was rarely taphonomic in origin (less than 0.05), but yielded a smaller frequency attributable to predation than the >10° strategy.

This finding suggests different potential approaches to assessing crushing predation, depending on the nature of the assemblage. In assemblages containing plentiful drilled shells (such as those in this study), VCA might be performed using the >10° strategy. This could maximize the ability of VCA to capture the frequency of damage due to crushing predation. This approach is predicated on the assumption that the >10° category generally reflects crushing predation in the gastropod assemblage in question. Thus, this strategy may be useful for comparing predation among assemblages of the same species (e.g., among *O. biplicata* assemblages where such damage has repeatedly been associated with predation). On the other hand, different gastropod species have different shell shapes and structure, different environmental preferences, and sometimes different predators. These factors may influence the particular types of damage caused by predation. For species that have never before been assessed with VCA, it would be wiser to use the full, twelve-category analysis to establish what types of damage represent predation.

Another approach suggested by the simplified VCA might even be applied to assemblages without abundant drilled shells: The >90° category, since such damage was extremely rarely attributable to taphonomy, could be assessed in a gastropod assemblage without using drilled shells to account for taphonomy. For example, an *O. biplicata* assemblage with few drilled shells could be compared to heavily drilled assemblages. As stated above, it is advisable to use the full VCA for a not-yet-examined species, to establish whether the damage categories are indeed attributable to predation.

Until we can further establish the applicability of the >10° and >90° damage categories to additional gastropod species, we recommend that the full VCA be used, particularly when assemblages are being compared across large geographic distances or through geologic time.

Consistency and Sample Size

The damage assessments among the resampled subsample of 55 Bamfield specimens were sufficiently consistent to deem the damage categories reliable. Even when the sample size was artificially inflated to tease out inconsistencies that may only manifest at higher sample sizes, only one potentially predatory damage category (columella damage) differed significantly among the iterations. Any other significant differences were detected in taphonomic categories, and thus would be unlikely to affect VCA results.

Fisher's exact test, as discussed above, is sensitive to sample size. Very small sample sizes are less likely to yield significant results, potentially obscuring real differences between drilled and undrilled shells. On the other hand, extremely large sample sizes can yield significant results even when the actual differences between drilled and undrilled samples are decidedly minor. Thus, it is useful to examine the effects of sample size on significance, using mock datasets to eliminate the other variables that affect significance.

For various sample-size levels (10, 20, 50, 100, 500, and 1000), we determined threshold differences, how disparate the drilled-undrilled damage frequencies have to be to yield a significant result at a given sample size. Obviously, this threshold will decrease as sample size increases (Table 5-9). At n = 10, 0% can be distinguished from 50%, and 20% can be distinguished from 80%. This is clearly insufficient to capture many meaningful differences in a shell assemblage. On the other end, at n = 1000, 0% can be distinguished from 0.6%, and 47.7% can be distinguished from 52.3%. In this case, these statistically distinguishable damage frequencies may not have significant biological meaning; it would be up to the researcher to determine this. For example, at n = 500, 46.8% and 53.2% can be distinguished statistically. Such minor differences in absolute frequency may not indicate major ecological differences. Thus, significance cannot be the sole basis for interpreting the results of VCA.

Based on the above sample-size thresholds, sample sizes between 100 and 500 are sufficient to discern major differences between drilled and undrilled shells. Unlike these mock datasets, drilled and undrilled samples are typically not equal; in the Bamfield dataset, there are approximately seven times more undrilled than drilled shells. However, with a drilled sample size of over 100, the samples are large enough to identify biologically meaningful differences in damage frequency. Thus, we recommend a minimum sample size of 100 for whichever sample (drilled or undrilled) is smaller. This is not to say that smaller sample sizes cannot capture meaningful trends, but simply that only more extreme differences in damage frequency may be detectable at smaller sample sizes.

MATERIALS AND METHODS II

Olivella biplicata from Bamfield, BC

Four separate collections of 1,067 empty *Olivella biplicata* shells (Figure 5-1a) were collected from Brady's Beach in Bamfield, British Columbia (Fig. 5-2a) during the summers of 2009 and 2010 (see Methods I).

Vermeij Crushing Analysis (see Methods I) was performed on the Bamfield *O. biplicata* assemblage using the original 12 damage categories. Fisher's exact test was used to compare the drilled and undrilled (non-pagurized) groups to determine whether any damage categories differed significantly between these groups. Damage profiles (bar graphs) were compared visually to identify which damage categories were possibly associated with crushing predation.

The VCA results and damage profiles of the Bamfield shells were them compared with previous results and profiles from *O. biplicata* from Torrey Pines in Southern California (Stafford and Leighton, 2011) (Fig 2b) to evaluate whether the results are consistent with the same species in another locality.

Bulliopsis marylandica from the Miocene St. Mary's Formation of Maryland

The extinct gastropod *Bulliopsis marylandica* was common in the Little Cove Point Member of the Miocene St. Mary's Formation of Maryland (Petuch and Drolshagen, 2010). The Little Cove Point Member spans the boundary between the Serravallian and Tortonian stages, approximately 11 Ma (Petuch and Drolshagen, 2010). The St. Mary's Formation formed during the St. Mary's subsea, when the now-Chesapeake Bay was a shallow-water embayment open to the Atlantic Ocean. The sandy bottoms led to the sandy cliffs that form the modern Chesapeake Bay's western shores.

B. marylandica is assigned to the Buccinoidea, but its familial designation is uncertain, being placed variably in the Buccinidae, Nassariidae, or another buccinoid family (Allmon, 1990; Haasl, 2000; Petuch and Drolshagen, 2010). Little is known about the ecology of *B. marylandica*. Its closest likely living relative, *Bullia* of Africa, lives in shallow sand environments, and like other buccinoids, is a semi-infaunal carnivore/scavenger (Brown, 1982;

Allmon, 1990). The species *Bullia laevissima*, in particular, has a similar shell shape to *B. marylandica*, but shell characters are not particularly informative of ecology in *Bullia* and related extinct buccinoids (Allmon, 1990). Regardless, it is reasonable to suspect that *B. marylandica* had a similar semi-infaunal, carnivorous lifestyle to living buccinoids such as *Bullia*. The paleoenvironment of the St. Mary's Formation, a shallow, sandy sea, supports this hypothesis for *B. marylandica*'s ecology.

The shell shape of *B. marylandica* is superficially quite similar to *O. biplicata*, being roughly olive-shaped (although some *B. marylandica* specimens have developed shoulders between whorls, which is not seen on *O. biplicata*). Although *B. marylandica* is not closely related to *O. biplicata* (of the Olivellidae, Olivoidea), the two are similar in size, shape, and putative ecology. Additionally, *B. marylandica* coexisted with a suite of crushing predators similar to those of modern shallow marine environments: portunid, cancrid, and xanthid crabs, stomatopod crustaceans (Rathbun, 1935), and durophagous fishes (pharyngeal jaw plates were found in the Little Cove Point bulk samples, along with unidentified crustacean claw fragments).

The *B. marylandica* specimens were collected near Cove Point, Maryland (Fig. 5-2c), during the springs of 2011 and 2012. The Little Cove Point Member exposure in this area can be resolved into distinct and traceable beds. Because of concerns with cliff erosion in the area, samples cannot be collected directly from the cliff walls. Fortunately, the individual beds can be readily identified in the large slump blocks that litter the cliff-base after storms. The *B. marylandica* specimens were sorted from multiple bulk samples, but there were not enough specimens to allow bed-by-bed analyses. Therefore, we combined all the Little Cove Point Member *B. marylandica* into a single sample of 543 specimens for Vermeij Crushing Analysis. This assemblage was compared to the Bamfield and Torrey Pines *O. biplicata* assemblages to determine whether the similarities in shell shape, environment, and predators are reflected in similar damage profiles (i.e., similar types and frequencies of damage attributable to crushing predation).

Examination of hermit crab habitation

The VCA method permits not only an analysis of crushing predation damage in a shell assemblage, but also examinations of hermit crab shell preference and potentially-predatory damage associated with hermit crab habitation.

To determine whether hermit crabs preferentially inhabited undrilled shells over drilled shells, the occurrences of hermit crab-associated damage were compared between drilled shells and all shells lacking a drillhole. Significantly greater occurrences of hermit crab-associated damage in one group indicate a preference.

In VCA, as described above, pagurized undrilled shells are removed from the dataset under the assumption that hermit crabs exposed inhabited shells to additional predatory and taphonomic damage relative to non-pagurized shells. The likelihood of this additional exposure can be tested by comparing the potentially predatory (not hermit crab-associated) damage categories between the pagurized and non-pagurized undrilled shell groups. Significantly greater occurrences of damage among pagurized shells suggest that hermit crab habitation did indeed expose shells to additional destruction. A lack of significant differences suggests that hermit crabs did not expose shells to additional destruction. Pagurized and non-pagurized shells were compared for both the Bamfield and Torrey Pines *O. biplicata* assemblages, as well as the Miocene *B. marylandica* assemblage.

Comparisons among successive Bamfield collections

The Bamfield assemblage was amassed from four separate collections taken in 2009 and 2010 (sample sizes between 68 and 387, before hermit crab correction). The drilled-undrilled occurrences of the original, uncombined damage categories in each individual collection were compared with one another (using Fisher's exact test) to evaluate the variation among collections drawn from the local gastropod population. The damage profiles were compared to assess whether the four collections were drawn from populations under a constant predation regime or under levels of predation that varied over space and/or time.

RESULTS II

Olivella biplicata from Bamfield, BC

Out of nine potentially predatory damage categories tested, damage was significantly greater ($p < 0.05$) among undrilled (non-pagurized) shells for eight categories (Fig. 5-4; Table 5-4). In five categories (apex removed, aperture damage 10°-90°, 90°-180°, >180°, and columella damage), the damage attributable to crushing predation was at least twice that attributable to taphonomy; i.e., the damage frequencies among drilled shells were very low (0 to 0.09). The

Estimated Minimum Crushing Mortality (all causes of death), based on aperture damage >10°, was 0.33 (Table 5-5). When drilled shells were excluded from the calculation, EMCM = 0.43. The drilling frequency of the assemblage was 0.24.

The *Olivella biplicata* assemblage from Torrey Pines (Stafford and Leighton, 2011) was reanalyzed according to the current protocol (using exclusive categories rather than inclusive categories; see Methods I). The Torrey Pines assemblage had a single category, apex damage, to encompass the two categories (apex abrasion and apex removed) used in the Bamfield assemblage. The damage profile (Fig. 5-5) was similar to that of the Bamfield assemblage (Fig. 5-4). Of seven potentially predatory damage categories examined, five were significantly more common among undrilled (non-pagurized) shells (Table 5-6). In four categories (aperture damage 90°-180°, >180°, columella damage, and hole in body whorl), the damage attributable to predation was at least twice that attributable to taphonomy (drilled frequencies ranging from 0 to 0.02) (Fig. 5-5). The EMCM (sum of the PF's of damage greater than 10°) is 0.18 (all causes of death) or 0.25 (undrilled shells only) (Table 5-5). The drilling frequency of the assemblage was 0.32.

Three of the significant categories (aperture damage 90°-180°, >180°, and columella damage) were also identified as such in the Bamfield assemblage. The Bamfield damage frequencies were overall higher than those of the Torrey Pines assemblage (Figures 5-4 and 5-5). Apex damage (both categories) in the Bamfield assemblage was partially attributable to predation, while apex damage was not significant in the Torrey Pines assemblage. The Bamfield EMCM is nearly twice that of Torrey Pines.

Bulliopsis marylandica **from the Miocene St. Mary's Formation of Maryland**

Due to the universal presence of apex abrasion and aperture abrasion, these two damage categories were not examined on *Bulliopsis marylandica*. Out of the remaining six potentially predatory damage categories, three categories (aperture damage 90°-180°, >180°, and columella damage) differed significantly at a p-value threshold of 0.05 (Table 5-7). Among the three categories with the lowest p-values, the difference in damage frequencies between the undrilled (non-pagurized) and drilled groups was greater than the differences observed in the other three categories (Fig. 5-6).

Apex damage was very infrequent in the *B. marylandica* assemblage, in contrast to the *O. biplicata* assemblage. Aperture damage 5°-10° was similar in frequency to the Bamfield *O. biplicata* assemblage, at about 0.80 for undrilled shells, and in all three assemblages (*B. marylandica*, Bamfield, and Torrey Pines) there was no significant difference for this damage category. Aperture damage 10°-90° was considerably higher in the *B. marylandica* assemblage, at over 0.45, but there was no difference between drilled and undrilled frequencies, in contrast to the two *O. biplicata* assemblages, which were both significant for this damage category. For the last three potentially-predatory damage categories (aperture damage 90°-80°, >180°, and columella damage), frequencies were higher in the *B. marylandica* assemblage than the *O. biplicata* assemblages, but were still significant in all three assemblages.

The EMCM, calculated as the sum of PF's of aperture damage greater than 10° (while aperture damage 10° to 90° was not significant for *B. marylandica*, this method is consistent with the *O. biplicata* assemblages; furthermore, the PF of aperture damage 10°-90° was very small, having a small impact on the calculated EMCM), was 0.26 (all causes of death) or 0.31 (undrilled shells only) (Table 5-5). The drilling frequency of the assemblage was 0.16.

Do pagurized shells differ from undrilled, non-pagurized shells?

To test whether hermit crabs preferentially inhabited or avoided drilled shells in the Bamfield *O. biplicata* assemblage, the occurrences of hermit crab-associated damage were compared between the drilled and undrilled (pagurized and non-pagurized combined) groups. All three damage categories (pinhole borings, boring trails, and *Helicotaphrichnus commensalis* borings) were significantly more common among undrilled shells (Fig. 5-7), suggesting that hermit crabs preferred undrilled shells and/or avoided drilled shells.

The same analyses of hermit crab habitation were performed for the Torrey Pines *O. biplicata* and Miocene *B. marylandica* assemblages. Within the Torrey Pines *O. biplicata* assemblage, all three hermit crab-associated damage categories occurred significantly more among undrilled shells than drilled shells (Fig. 5-8). For *B. marylandica,* only boring trails were significantly more common in the undrilled shells, giving moderate evidence that undrilled shells were preferred over drilled shells (Fig. 5-9). There was no significant difference in the *H. commensalis* trace, which is a positive sign of hermit crab habitation.

If hermit crabs did preferentially inhabit undrilled shells, they may have exposed the undrilled shell assemblage to additional predatory and taphonomic damage. To test this, the occurrences of the potentially-predatory damage categories were compared between pagurized and non-pagurized undrilled shells. Out of the nine categories assessed in the Bamfield assemblage, three differed significantly (aperture damage 90°-180°, >180°, and hole in body whorl) (Fig. 5-10). An additional category (columella damage) had a low p-value (0.06) relative to the remaining categories. Of these four categories, three (90°-180°, >180°, and columella damage) types of damage were *less common* among pagurized shells. Only one category (hole in body whorl) was significantly more frequent among pagurized shells.

The above analyses were also done for the Torrey Pines and the *B. marylandica* assemblages. Within the Torrey Pines undrilled shells, comparing the potentially predatory damage categories between the pagurized and non-pagurized groups, two of the eight categories (aperture damage >180° and columella damage) differed significantly (Fig. 5-11); an additional category (aperture damage 90°-180°) had a p-value of 0.08, considerably lower than those of the remaining categories. In the three categories with the lowest p-values, damage was *less common* among pagurized shells. Within the undrilled *B. marylandica* shells, out of the seven categories examined, two (aperture damage >180° and hole in body whorl) were significantly *more common* among pagurized shells (Fig. 5-12).

Comparisons among successive Bamfield collections

The four collections that make up the Bamfield *O. biplicata* assemblage (2009, 2010-1, 2010-2, and 2010-3) were analyzed individually to detect variation within the overall assemblage (Table 5-8). Collection 2010-2 was most similar to the combined results, sharing five of the seven significant categories. Neither aperture abrasion nor hole in body whorl was significant among any of the collections. Aperture damage 90°-180° was significant in three of the four collections.

The EMCM of the four collections were fairly consistent. When EMCM was calculated using drilled and undrilled shells, collection 2010-2 differed from the others, having a lower EMCM. When EMCM was calculated using only undrilled shells, collection 2010-3 differed markedly from the others (0.93).

DISCUSSION II

Comparison of *Olivella biplicata* from Bamfield and Torrey Pines and St. Mary's *Bulliopsis marylandica*

The most notable difference between the Bamfield and Torrey Pines assemblage is that the damage frequencies are higher overall in the Bamfield assemblage. Otherwise, while there are some differences in which categories are significant, the same pattern of damage emerges: the lesser apertural damage categories are quite frequent (over 0.50) and are largely attributable to taphonomy. The more severe apertural damage categories are less frequent, but when they do occur they are largely attributable to crushing predation. The fact that the pattern first observed in Stafford and Leighton (2011) reoccurs in a new assemblage suggests that VCA is capturing a real picture of the taphonomic and predatory conditions of the shell assemblage. Both assemblages share a common species and a common environment, with likely many common predators, so it is unsurprising that the types of taphonomic and predatory damage observed are the same. This suggests that the observed differences between the two assemblages are probably caused by a difference in predation intensity.

Interestingly, the comparison of these two assemblages appears to defy the notion that predation is higher in lower latitudes (Vermeij, 1977; Palmer, 1979; Vermeij et al., 1980; Bertness and Cunningham, 1981; Vermeij, 1987). Estimated crushing predation, based solely on VCA, is higher in the Bamfield assemblage (48.8°N) than in Torrey Pines (32.9°N), contrary to the expected latitudinal predation gradient. In addition, the Bamfield *Olivella biplicata* are larger than those of Torrey Pines. A potential explanation for this counterintuitive result it that ecosystem health may be better in Bamfield; the Bamfield area has a much lower human population and level of development than Torrey Pines (north of San Diego) and thus may be less affected by pollution and overfishing. VCA may prove extremely informative when applied to numerous shell assemblages along a gradient, in this case the latitudinal gradient along the North American Pacific coast.

The St. Mary's *Bulliopsis marylandica* assemblage, separated from the *O. biplicata* assemblages evolutionarily, temporally, and geographically, has a remarkably similar pattern of taphonomic and predatory damage to the other two assemblages. In particular, aperture damage >90° is attributable to predation in all assemblages. This is likely due to both the similarity in shell shape between *O. biplicata* and *B. marylandica* and similarities in the predatory techniques of their crushing predators. The Miocene sea of mid-Atlantic North America had an effectively modern suite of crushing predators, including crabs in the families Portunidae, Cancridae, and Xanthidae (Rathbun, 1935). These predators are known to produce aperture damage during predatory attacks in modern systems (Stafford et al. (in review) and references therein), so it is unsurprising that predatory damage in the Miocene was similar to that observed in the modern. The fact that VCA accurately captures this similarity validates its use in identifying and quantifying predatory damage, even in the fossil record.

In the *B. marylandica* assemblage, apex damage is extremely infrequent. This may be due to shell morphological differences: the *B. marylandica* shells have a more robust, calcified apex, whereas that of *O. biplicata* is hollow, leading to more frequent and catastrophic damage. It is also possible that predators of *B. marylandica* did not attack the apex when crushing (at least some apex damage in the Bamfield assemblage is attributable to crushing). Also, the less severe aperture damage categories, AD 5°-10° and AD 10°-90° were effectively equal between drilled and undrilled shells in the *B. marylandica* assemblage, indicating that the damage was due entirely to taphonomy. In both *O. biplicata* assemblages, AD 10°-90° was significant, and AD 5°-10° was nonsignificantly higher in undrilled shells. However, each of these damage types was overall more frequent in the *B. marylandica* assemblage, so it is conceivable that predation-induced damage may have been masked by taphonomy. Another explanation is that predators only produced more extreme damage during attack (>90), perhaps because *B. marylandica* could retract deep enough into its shell to survive less extreme aperture damage. Shell-aperture-peeling predators peel more deeply into the shell to access deeply-retracting gastropods (Stafford et al. (in review) and references therein).

VCA and hermit crab habitation

The comparisons of hermit crab-associated damage frequencies between the drilled and undrilled samples in all three assemblages confirm the findings of others that hermit crabs have a strong preference for undrilled shells (Pechenik and Lewis, 2000; Pechenik et al., 2001). For the undrilled shells among the three assemblages, the frequency of *Helicotaphrichnus commensalis* borings was similar: somewhat more than 0.3. The frequencies of boring trails (probably borings by spionid worms, and maybe clionid sponges) and pinhole borings (possibly predatory borings by muricid gastropods or octopods) differed more among the three assemblages (pinholes were not observed in the *B. marylandica* assemblage, though this may have been due to poor preservation).

The pagurized (i.e., bearing hermit crab-associated damage) and non-pagurized undrilled shells were compared for all the damage categories. The data show that for the *O. biplicata* assemblages, damage frequencies are in fact *lower* among pagurized shells. Despite the additional exposure to taphonomic forces and predation, potentially-predatory damage is more common on shells not exhibiting signs of hermit crab habitation, with the exception of a few categories. The categories that are more frequent in pagurized *O. biplicata* are apex removal and hole in body whorl (for both assemblages), and AD 5°-10° and 10°-90° (for the Bamfield assemblage only). Only in the case of hole in body whorl (Bamfield) is the frequency significantly greater for pagurized shells. In all other cases, damage is either nonsignificant or significantly greater in nonpagurized shells. This is consistent with Stafford and Leighton (2011), where EMCM *increased* when hermit crab habitation was accounted for.

This difference (or non-difference) in damage between pagurized and nonpagurized shells may indicate that crushing predation does not occur frequently on hermit crabs, perhaps because the hermit crabs are less likely to encounter, or are more likely to escape, predators (Stafford, in review). Another explanation is that hermit crabs prefer shells that are not only undrilled but also undamaged, and that crushing predation on hermit crabs occurs at equal or lower frequencies than on live gastropods.

Unlike *O. biplicata*, damage frequencies were higher for pagurized *B. marylandica*, but not significantly so. The hermit crabs may have exposed the *B. marylandica* shells to additional taphonomic or predatory damage, but the slight increase on pagurized shells does not change the overall pattern of damage.

For *O. biplicata,* it is likely that either crushing predation is/was not particularly common on the hermit crabs, or crushing predation occurs/occurred at a similar rate on hermit crabs, but the hermit crabs tended to start with undamaged shells. Thus, it may not be necessary to remove pagurized shells from the assemblage when performing VCA, particularly in cases of low sample size. However, the dynamics of the gastropod-hermit crab-predator system likely vary depending on the environments and species involved, so we recommend that damage on the pagurized and nonpagurized undrilled shells be assessed before deciding whether to exclude pagurized shells.

In fact, such additional data on hermit crab habitation, pagurization, and predation would be valuable in itself for the study of predation on hermit crabs.

Comparison among successive Bamfield collections

The four collections within the Bamfield *O. biplicata* assemblage were compared to explore the variation in predation among the collections (Table 5-8). While there are particular differences in the damage frequencies, the patterns of aperture damage among the collections are consistent: for aperture damage >10°, damage is consistently greater among undrilled shells than drilled shells, and damage is low or nonexistent among drilled shells. For each calculation of EMCM (drilled + undrilled shells or undrilled shells only), three of the four collections yielded similar values.

When EMCM was calculated using drilled and undrilled shells, three of the collections had values of approximately 0.35, meaning that 35% of the total assemblage owed its cause of death to crushing predation. One collection, 2010-2, had a lower EMCM (0.27). This lower EMCM is likely not a function of drilling frequency, as 2010-2 had only the second highest drilling frequency of the four collections.

When EMCM was calculated using only undrilled shells, three of the collections had values of approximately 0.40, while the fourth (2010-3) had an extremely high value, 0.93. This may be in part due to 2010-3 having the highest drilling frequency, 0.61 (the only collection to contain more drilled shells than undrilled shells).

The similarities among the collections are unsurprising, as the shells most likely originated from the same environment and population, given the relatively small collection area (a 0.5-km stretch of beach). However, the collections are by no means identical in damage frequencies and EMCM's.

One explanation might be that the differences among the collections reflect temporal differences in predation on the gastropod population over the period of collection. Because predation has not been measured directly in the gastropod population, we do not know how variable predation was during the collection times, in terms of magnitude of variation and frequency of fluctuation. We did observe major declines in the population of *Cancer productus* in the Bamfield area in 2012 compared with previous years and with 2013, so temporal variation is not unexpected. At any given time, the dead shell assemblage is time-averaged to some degree.

This time averaging may be expected to reduce the temporal variation in predation in the live gastropod community; however, see Dietl and Kosloski (2013) for further considerations on the effects of time averaging.

Another possibility is that taphonomic factors caused some of the variation among the collections. By taphonomy, here, we are not just referring to the taphonomic damage on the shells (which is accounted for in VCA), but also the post-mortem factors that influence which shells end up in an assemblage. Differential burial, differential transport, and differential hermit crab habitation can lead to assemblages that do not reflect the overall population.

Without access to the dead shells that are buried, rather than transported and deposited on the beach, it is difficult to tell whether some shells are more likely to be buried than others. Similarly, while there has been little work on the entrainment and transport of gastropod shells, Molinaro et al. (2013) found no evidence that the presence of a predatory drillhole affects the velocity of entrainment (and thus the potential for transport) of an *O. biplicata* shell. Molinaro et al. (13) did not examine the entrainment of shells with varying degrees of apertural damage. If shells with apertural damage entrain at lower velocities, for instance, they may be more likely to be transported away from their original location. Such differential entrainment and transport could yield multiple assemblages from the same dead shell population: some assemblages would have a higher proportion of damaged shells, while other assemblages would have a lower proportion.

Importantly, we found that damage 90° and deeper was consistently attributable to predation. This pattern held up regardless of taxon (predation patterns were similar for *O. biplicata* and *B. marylandica*), age, and locality (patterns were nearly identical for *O. biplicata* between the Bamfield and Torrey Pines assemblages). Furthermore, the predatory origin of > 90° aperture damage was discernible at low sample sizes and through the ecological filter of hermit crab habitation. This consistency reinforces two points: the validity of Vermeij Crushing Analysis as a method for examining predation and identifying predatory damage; and the origin of such severe apertural damage in crushing attacks.

CONCLUSIONS

Vermeij Crushing Analysis is a valid and useful method of examining crushing predation in gastropod assemblages. A simplified protocol for VCA shows promise in analyzing assemblages of the same species and habitat, but we recommend using the full VCA protocol until the types of predation attributable to predation are better established among various species in different environments. A sample size of at least 100 drilled shells and 100 undrilled shells is sufficient for detecting statistical differences in damage categories, but the ecological significance of such differences must also be assessed independent of p-values.

A comparison of two modern *Olivella biplicata* assemblages from the North American Pacific coast and one fossil *B. marylandica* assemblage from the Miocene of Maryland found similar patterns of predatory fragmentation, with severe apertural damage being attributable to predation. This pattern was consistent regardless of non-predatory factors such as taxon, sample size, locality, and age.

FIGURES

Figure 5-1. A. *Olivella biplicata* with naticid predatory drillhole, from Bamfield, British Columbia, Canada. B. *Bulliopsis marylandica* from the Miocene St. Mary's Formation of Maryland, USA. C-J. Potentially-predatory damage categories, shown on *O. biplicata* from Bamfield, BC: C. Apex removed (*O. biplicata*); D. Aperture abrasion; E. Aperture damage 5°-10°; F. Aperture damage 10°-90°; specimen also bears *Helicotaphrichnus commensalis* spionid worm boring (arrow); G. Aperture damage 90°-180°; H. Aperture damage greater than 180°; J. Columella damage. K. Boring trails; specimen is extensively bored.

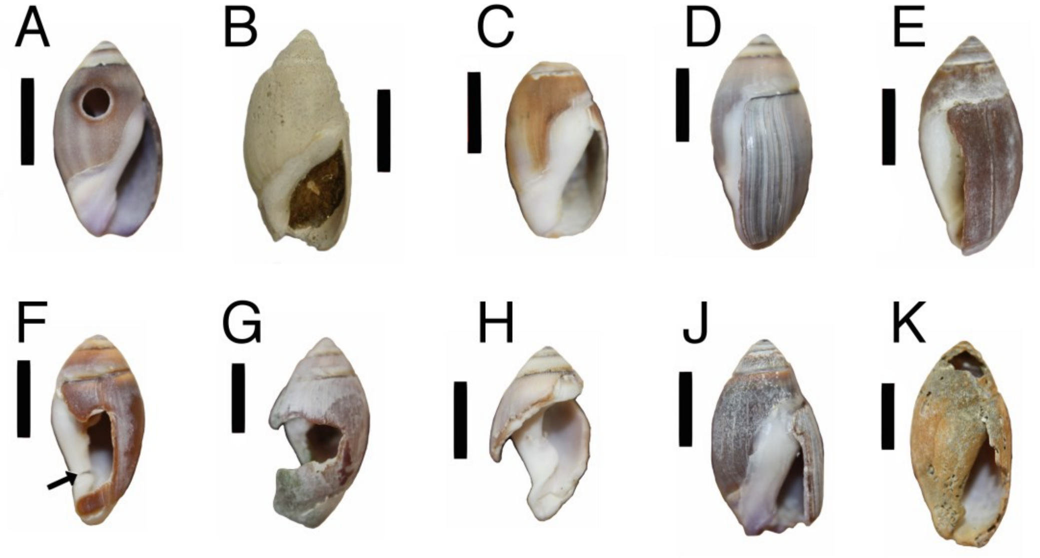


Figure 5-2. Locality maps; stars indicate collection locations. A. Bamfield, British Columbia, Canada; B. Torrey Pines State Beach, California, USA; C. Miocene St. Mary's Formation of Maryland, USA.

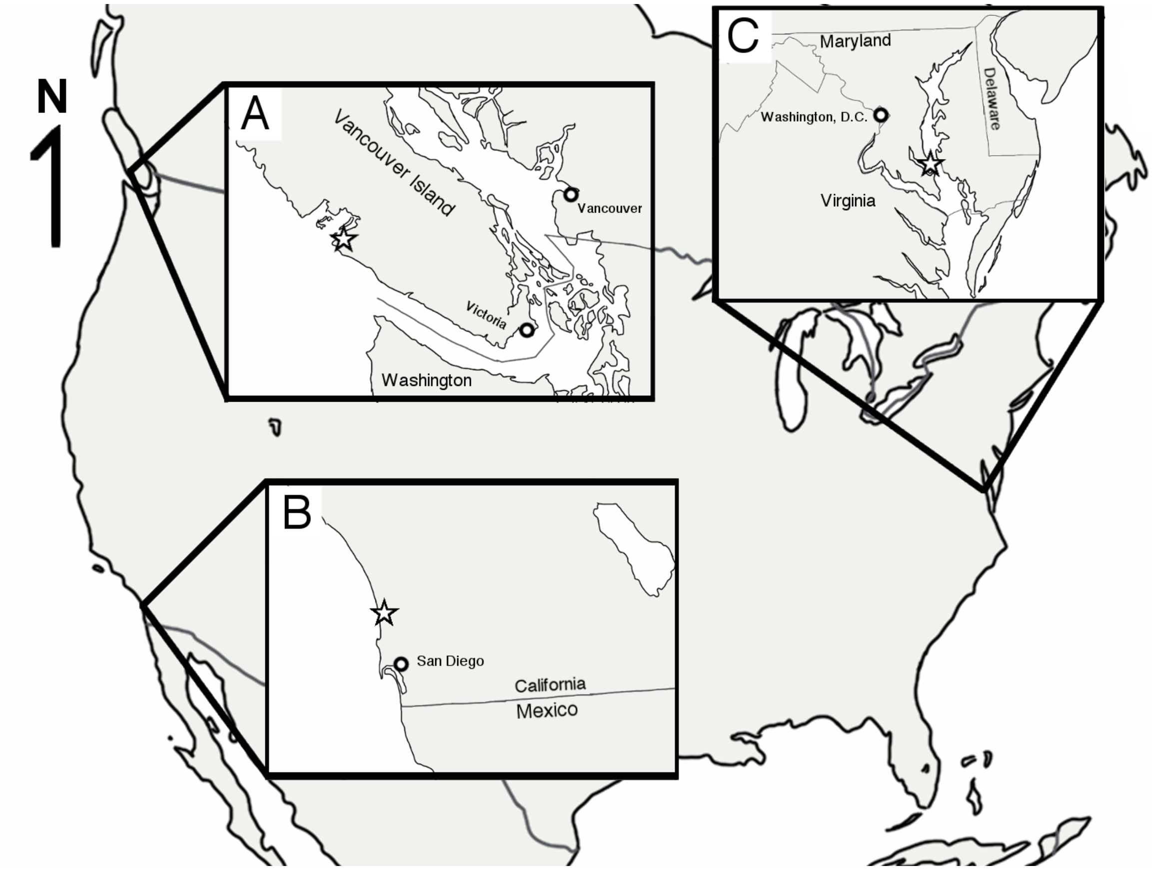


Figure 5-3. Comparison of three damage lumping strategies using the Bamfield *Olivella biplicata* dataset. Black stars indicate a significant difference ($p < 0.05$) in damage occurrence between drilled and undrilled shells.

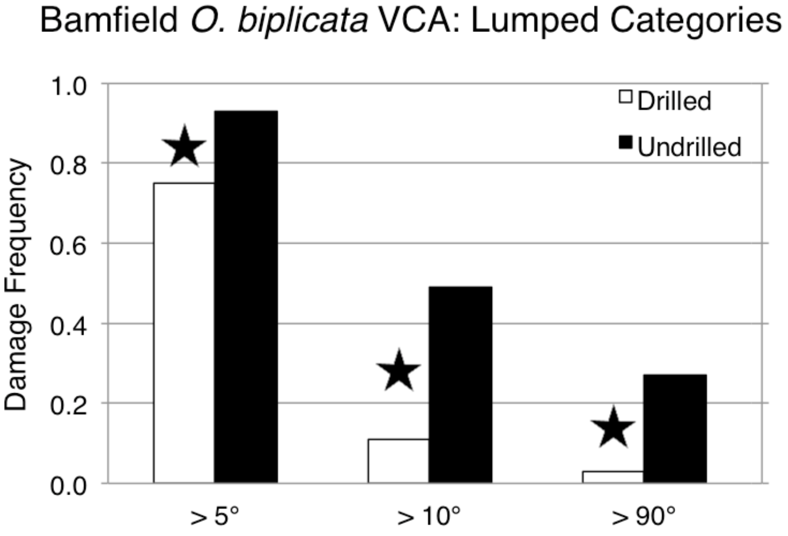


Figure 5-4. Damage profile comparing drilled and undrilled (non-pagurized) *Olivella biplicata* from Bamfield, BC. Black stars indicate a significant difference ($p < 0.05$) in damage occurrence between drilled and undrilled shells.

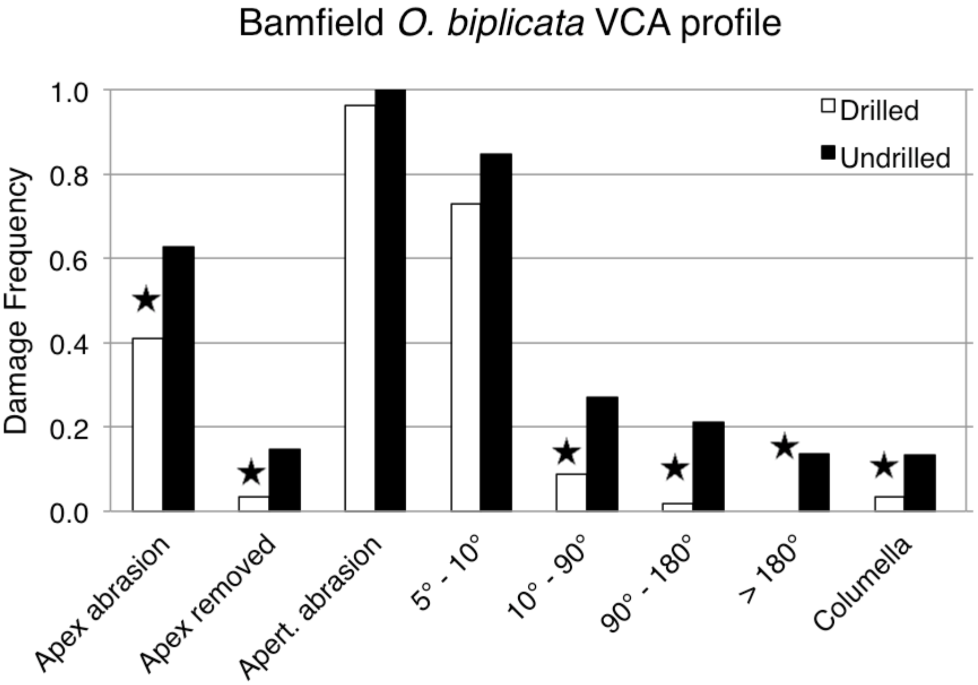


Figure 5-5. Damage profile comparing drilled and undrilled (non-pagurized) *Olivella biplicata* from Torrey Pines, CA (data from Stafford and Leighton (2011). Black stars indicate a significant difference ($p < 0.05$) in damage occurrence between drilled and undrilled shells.

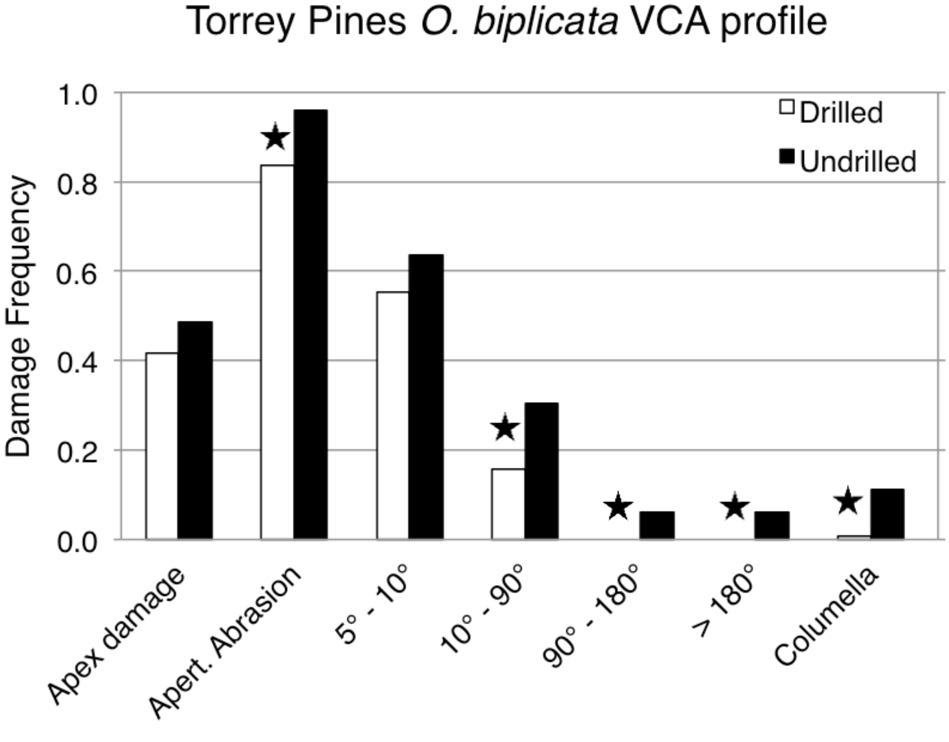


Figure 5-6. Damage profile comparing drilled and undrilled (non-pagurized) *Bulliopsis marylandica* from the Miocene St. Mary's Formation of Maryland. Black stars indicate a significant difference ($p < 0.05$) in damage occurrence between drilled and undrilled shells.

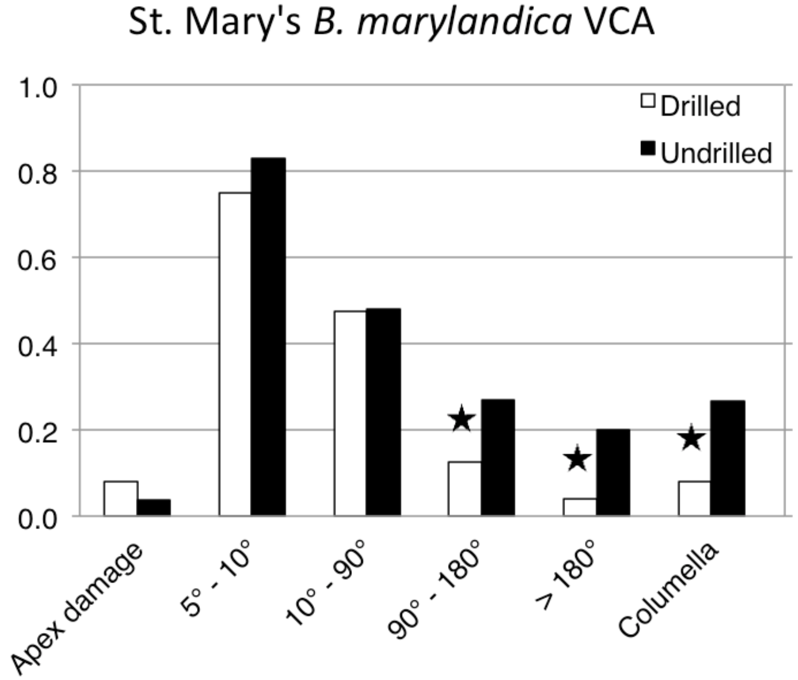


Figure 5-7. The frequencies of hermit crab-associated damage categories for undrilled and drilled *Olivella biplicata* (Bamfield, BC), as a proxy for the relative frequencies of pagurization of shells. Black stars indicate a significant difference ($p < 0.05$) in damage occurrence between drilled and undrilled shells.

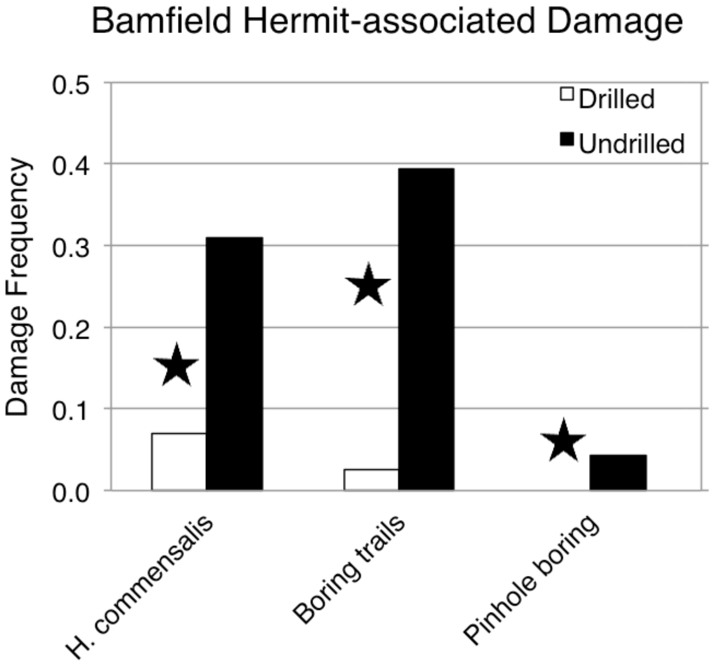


Figure 5-8. The frequencies of hermit crab-associated damage categories for undrilled and drilled *Olivella biplicata* (Torrey Pines, CA), as a proxy for the relative frequencies of pagurization of shells. Black stars indicate a significant difference ($p < 0.05$) in damage occurrence between drilled and undrilled shells.

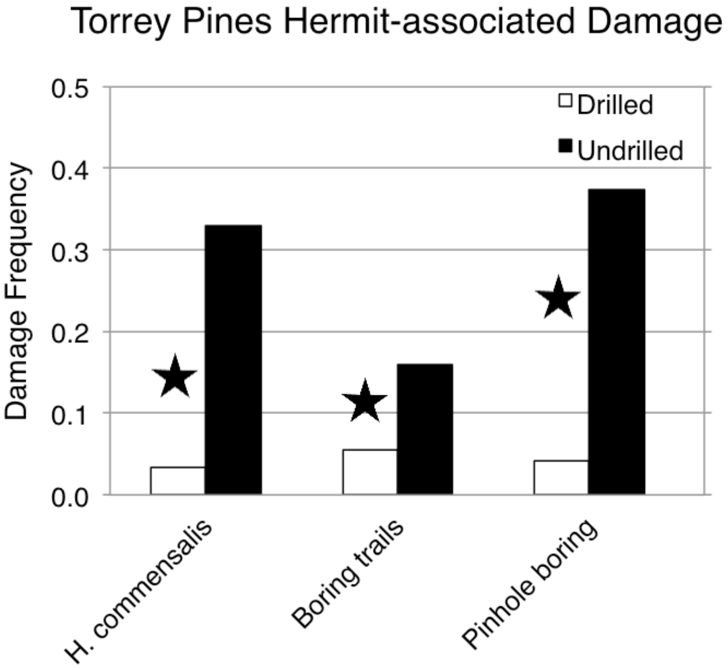


Figure 5-9. The frequencies of hermit crab-associated damage categories for undrilled and drilled *Bulliopsis marylandica* (Miocene St. Mary's Formation, MD), as a proxy for the relative frequencies of pagurization of shells. The black star indicates a significant difference ($p < 0.05$) in damage occurrence between drilled and undrilled shells.

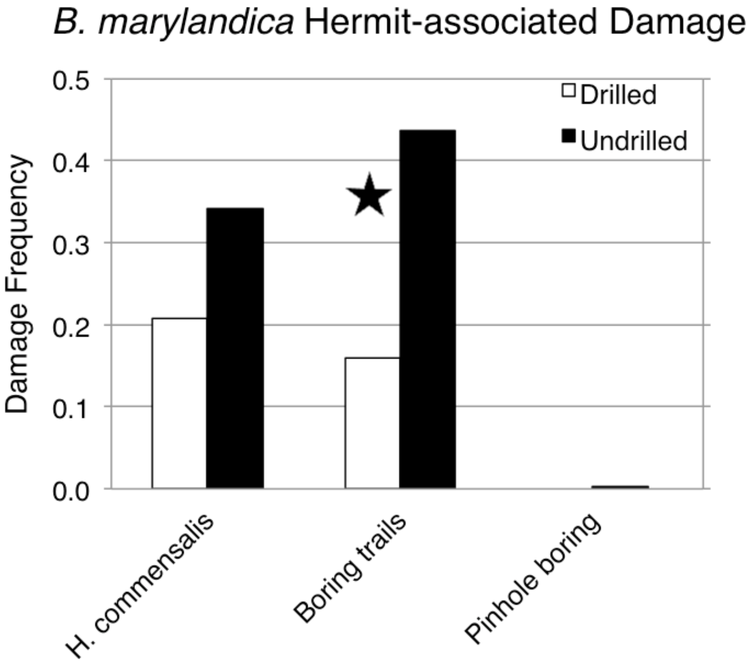


Figure 5-10. Damage frequencies compared between non-pagurized (black) undrilled and pagurized (gray) undrilled *Olivella biplicata* (Bamfield, BC). Drilled shell damage frequencies (white) are shown for comparison. Black stars indicate significant differences ($p < 0.05$) in damage occurrence between pagurized and non-pagurized shells.

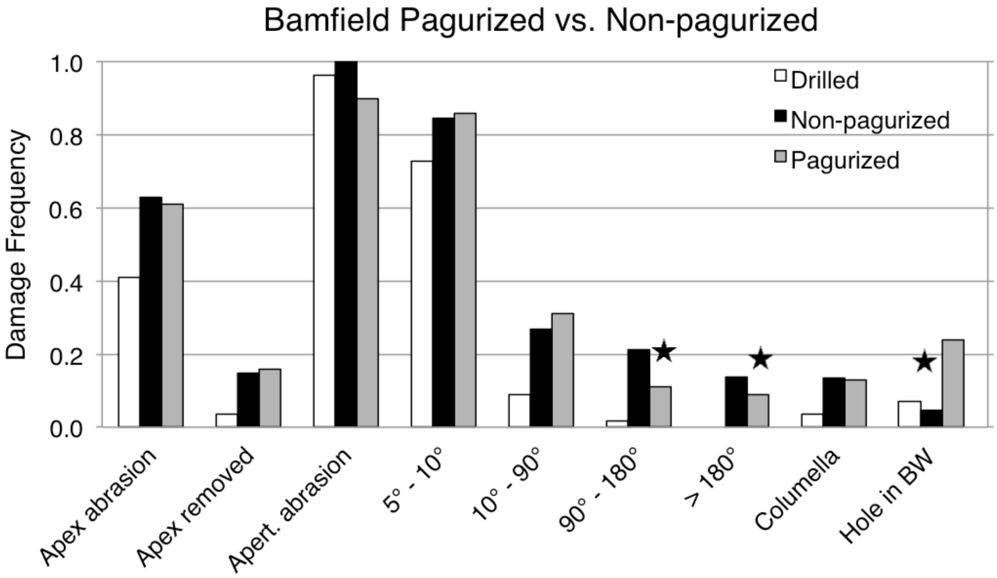


Figure 5-11. Damage frequencies compared between non-pagurized (black) undrilled and pagurized (gray) undrilled *Olivella biplicata* (Torrey Pines, CA). Drilled shell damage frequencies (white) are shown for comparison. Black stars indicate significant differences ($p < 0.05$) in damage occurrence between pagurized and non-pagurized shells.

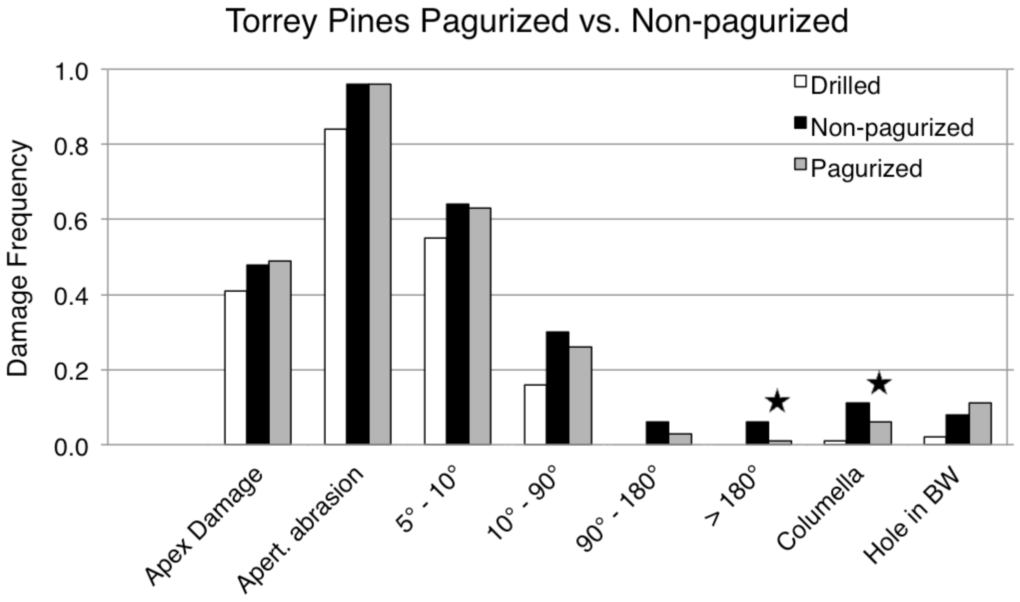
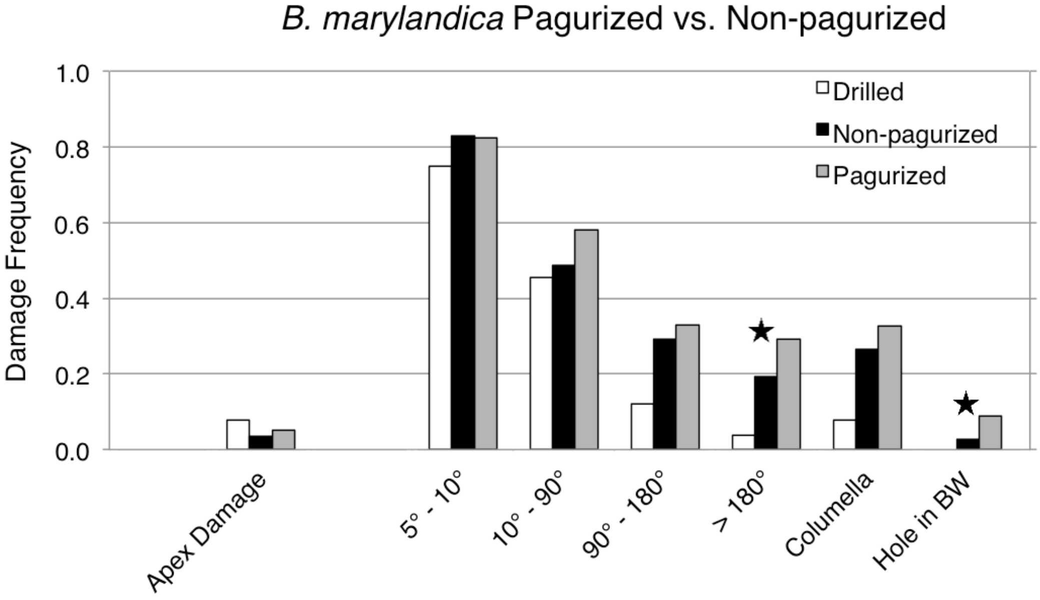


Figure 5-12. Damage frequencies compared between non-pagurized (black) undrilled and pagurized (gray) undrilled *Bulliopsis marylandica* (Miocene St. Mary's Formation, MD). Drilled shell damage frequencies (white) are shown for comparison. Black stars indicate significant differences ($p < 0.05$) in damage occurrence between pagurized and non-pagurized shells.



TABLES

Table 5-1. Simplified Vermeij Crushing Analysis using three different lumping strategies: all damage greater than 5°; all damage greater than 10°; and damage 5°-90° versus damage greater than 90°. P-values less than 0.05 indicate a statistically significant difference between drilled and undrilled shells.

Bamfield Lumped Categories

		> 5°	>10°	5°- 90°	> 90°
Drilled	Damaged	89	13	86	3
	Undamaged	29	105	32	115
	Frequency	*0.75*	*0.11*	*0.73*	*0.03*
Undrilled	Damaged	711	373	500	211
	Undamaged	57	395	268	557
	Frequency	*0.93*	*0.49*	*0.65*	*0.27*
	p-value	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Table 5-2. Comparisons among three iterations of a single subsample of 55 specimens. Top: the original 55-specimen samples. Bottom: the original samples multiplied times ten to simulate a sample size of 550 specimens. Plus signs + indicate significant differences between iterations.

Bamfield Subsample Consistency

n = 55	Drilled	Apex abrasion	Apex removed	Aperture abrasion	5 - 10	10 - 90	90 - 180	180 +	Columella damaged	Hole in BW	Pinhole	*Helico. commensalis*	Boring trails
1 v 2	no significant differences												
1 v 3													
2 v 3													
n = 550													
1 v 2		+	+	+					+				
1 v 3			+	+					+				
2 v 3		+	+									+	

Table 5-3. Significance thresholds at different sample sizes. Top: Versus Zero method of simulating samples. Bottom: Inverse Frequency method of simulating samples.

VCA Sample Size Thresholds

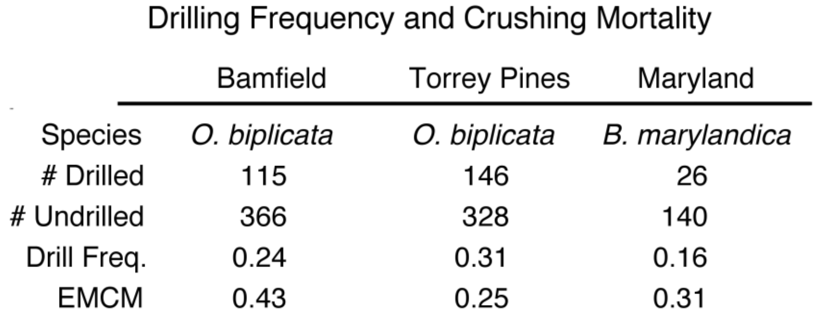
	n = 10			n = 20			n = 50			n = 100			n = 500			n = 1000		
Versus Zero																		
	A	B	p-value	A	B	p-value	A	B	p-value	A	B	p-value	A	B		A	B	p-value
Damaged	0	5	0.033	0	5	0.047	0	6	0.027	0	6	0.029	0	6	0.031	0	6	0.031
Undamaged	10	5		20	15		50	44		100	94		500	494		1000	994	
Frequency	0	0.50		0	0.25		0	0.12		0	0.06		0	0.012		0	0.006	
Inverse Frequency																		
	A	B	p-value	A	B	p-value	A	B	p-value	A	B	p-value	A	B	p-value	A	B	p-value
Damaged	2	8	0.023	6	14	0.026	19	31	0.027	42	58	0.034	234	266	0.050	477	523	0.044
Undamaged	8	2		14	6		31	19		58	42		266	234		523	477	
Frequency	0.20	0.80		0.30	0.70		0.38	0.62		0.42	0.58		0.468	0.532		0.477	0.523	

Table 5-4. Vermeij Crushing Analysis results for *Olivella biplicata* from Bamfield, British Columbia, Canada.

Bamfield *O. biplicata* VCA

		Apex abrasion	Apex removed	Aperture abrasion	5° - 10°	10° - 90°	90° - 180°	180° +	Columella damaged
Drilled	damaged	46	4	26	75	10	2	0	4
n = 115	undamaged	66	111	1	28	103	113	115	111
	frequency	*0.41*	*0.03*	*0.96*	*0.73*	*0.09*	*0.02*	*0.00*	*0.03*
Undrilled	damaged	196	54	28	154	67	67	50	49
n = 366	undamaged	116	312	0	28	182	249	316	317
	frequency	*0.63*	*0.15*	*1.00*	*0.85*	*0.27*	*0.21*	*0.14*	*0.13*
	$p < 0.05$	yes	yes	no	no	yes	yes	yes	yes

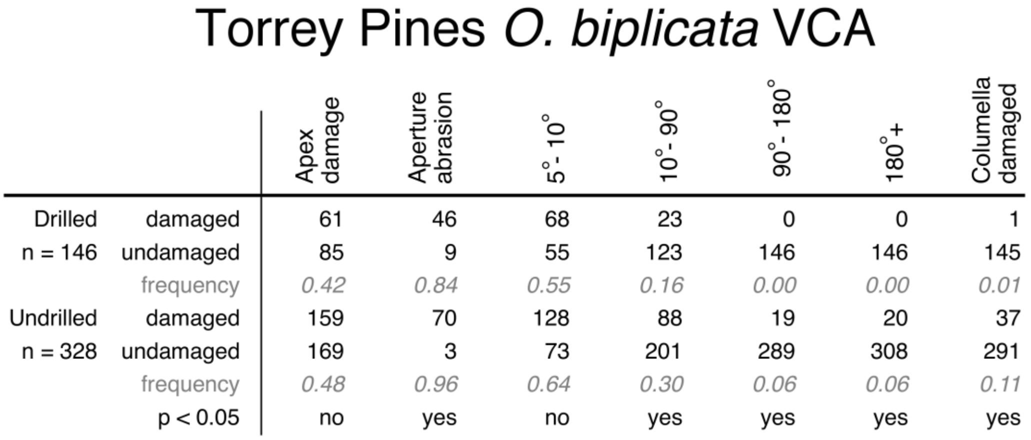
Table 5-5. Specimen counts, drilling frequency, and Estimated Minimum Crushing Mortality (EMCM) for gastropod assemblages from the three localities.



Drilling Frequency and Crushing Mortality

	Bamfield	Torrey Pines	Maryland
Species	*O. biplicata*	*O. biplicata*	*B. marylandica*
# Drilled	115	146	26
# Undrilled	366	328	140
Drill Freq.	0.24	0.31	0.16
EMCM	0.43	0.25	0.31

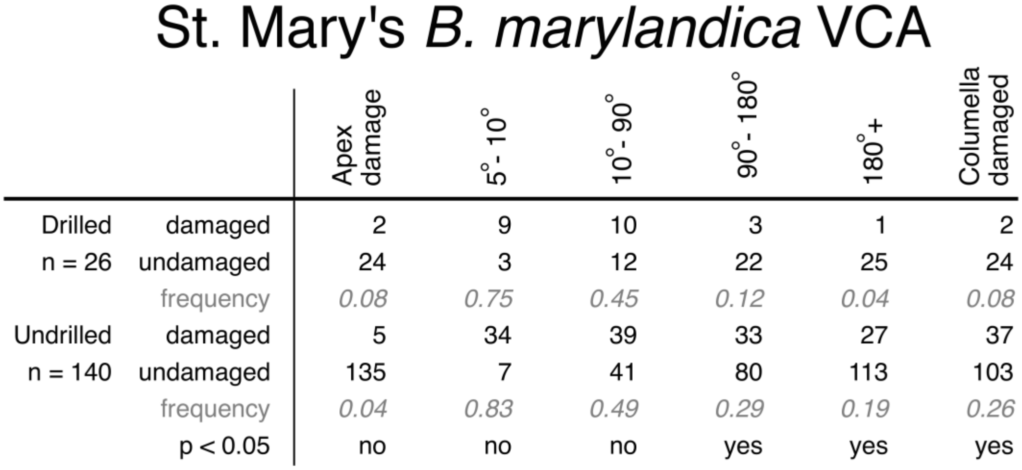
Table 5-6. Vermeij Crushing Analysis results for *Olivella biplicata* from Torrey Pines, California, USA.



Torrey Pines *O. biplicata* VCA

		Apex damage	Aperture abrasion	5° - 10°	10° - 90°	90° - 180°	180°+	Columella damaged
Drilled	damaged	61	46	68	23	0	0	1
n = 146	undamaged	85	9	55	123	146	146	145
	frequency	*0.42*	*0.84*	*0.55*	*0.16*	*0.00*	*0.00*	*0.01*
Undrilled	damaged	159	70	128	88	19	20	37
n = 328	undamaged	169	3	73	201	289	308	291
	frequency	*0.48*	*0.96*	*0.64*	*0.30*	*0.06*	*0.06*	*0.11*
	$p < 0.05$	no	yes	no	yes	yes	yes	yes

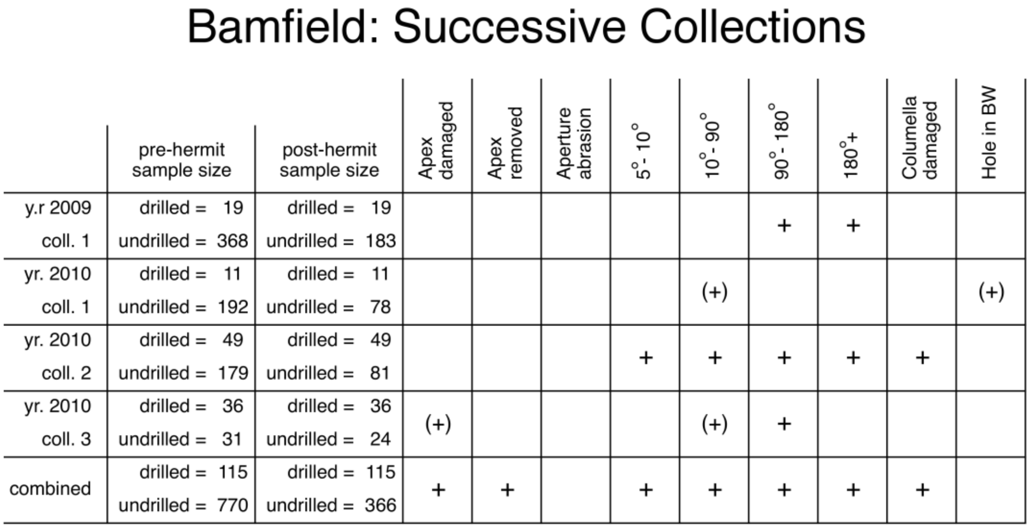
Table 5-7. Vermeij Crushing Analysis results for fossil *Bulliopsis marylandica* from the Miocene St. Mary's Formation of Maryland, USA.



St. Mary's *B. marylandica* VCA

		Apex damage	5°- 10°	10°- 90°	90°- 180°	180°+	Columella damaged
Drilled	damaged	2	9	10	3	1	2
n = 26	undamaged	24	3	12	22	25	24
	frequency	0.08	0.75	0.45	0.12	0.04	0.08
Undrilled	damaged	5	34	39	33	27	37
n = 140	undamaged	135	7	41	80	113	103
	frequency	0.04	0.83	0.49	0.29	0.19	0.26
	p < 0.05	no	no	no	yes	yes	yes

Table 5-8. Comparisons between the four separate collections of *Olivella biplicata* in the Bamfield, BC assemblage. Plus signs + indicate a significant difference (p-value less than 0.05) between drilled and undrilled damage frequencies based on Vermeij Crushing Analysis. Parenthesized plus signs (+) indicate p-values of less than 0.1.



Bamfield: Successive Collections

	pre-hermit sample size	post-hermit sample size	Apex damaged	Apex removed	Aperture abrasion	5°- 10°	10°- 90°	90°- 180°	180°+	Columella damaged	Hole in BW
y.r 2009 coll. 1	drilled = 19 undrilled = 368	drilled = 19 undrilled = 183						+	+		
yr. 2010 coll. 1	drilled = 11 undrilled = 192	drilled = 11 undrilled = 78					(+)				(+)
yr. 2010 coll. 2	drilled = 49 undrilled = 179	drilled = 49 undrilled = 81				+	+	+	+	+	
yr. 2010 coll. 3	drilled = 36 undrilled = 31	drilled = 36 undrilled = 24	(+)				(+)	+			
combined	drilled = 115 undrilled = 770	drilled = 115 undrilled = 366	+	+		+	+	+	+	+	

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CHAPTER 6

DRILLING, DUROPHAGY, AND A TEST FOR TROPHIC CASCADES IN THE MIOCENE ST. MARY'S FORMATION[4]

INTRODUCTION

The effects of predation extend beyond the direct predator-prey interaction. A predator species can have a positive effect on the population of a prey species at a lower trophic level by preying upon an intermediate predator, a phenomenon termed a trophic cascade (Hairston et al., 1960; Pinnegar et al., 2000). Cascading effects are not limited to lethal predation. In trait-mediated indirect interactions (TMII), predators can have nonlethal effects on their prey's behavior; for example causing the prey to hide instead of foraging or mating (Werner and Peacor, 2003). Trophic cascades and TMIIs have been demonstrated many times in modern systems, among a variety of predator and prey species (Lima and Dill, 1990; Lima, 1998; Trussel et al., 2002; Trussel et al., 2003; Trussel et al., 2004; Chattopadhyay and Baumiller, 2007; Freeman and Hamer, 2009; Large and Smee, 2010). The present study uses the fossil record to examine potential trophic cascades in ancient predator-prey systems.

Fossil assemblages can expand the scope of predation studies by allowing researchers to follow trends in predation through time and see how predation influences the evolution of predator and prey taxa. It is difficult to assess TMIIs in fossil communities because many examples of predation and other foraging behaviors are rarely preserved in the fossil record. However, in instances where predatory behavior is recorded in trace fossils at multiple trophic levels, TMIIs may be assessed. Chattopadhyay and Baumiller (2010) hypothesized that TMIIs may be detected in molluscan assemblages that contain molluscan drilling predators. Naticid gastropods drill other mollusks, but are themselves preyed upon by durophagous predators such as crabs. When naticids encounter their own crushing predators, they may reduce their foraging, or may be interrupted before completing a drillhole. Chattopadhyay and Baumiller (2010) predicted that when crushing predation on naticids is greater, drilling frequencies and/or drilling success should be lower. They tested this prediction in six Plio-Pleistocene assemblages, using repair frequency as a proxy for crushing predation intensity on naticid gastropods. Repair frequency was compared with the drilling frequencies of gastropod and bivalve prey, and the

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[4] A version of this chapter has been accepted with revisions. Stafford and Leighton, *Paleobiology*

authors found that when repairs on naticids were more frequent, drilling predation tended to be less frequent and less successful (Chattopadhyay and Baumiller, 2010). This suggested that naticids indeed reduced their foraging, and were less successful, when under more intense crushing predation pressure. This was also consistent with their work in a modern setting: using crabs, drilling muricid gastropods, and mussel prey; they observed that drilling frequency and drilling success were lower in the presence of crabs (Chattopadhyay and Baumiller, 2007). In the present study, we apply Chattopadhyay and Baumiller's (2010) hypothesis to a similar fossil molluscan assemblage from the Miocene St. Mary's Formation of Maryland to further test whether TMIIs can be observed.

Chattopadhyay and Baumiller (2010) used repair frequency as a proxy for crushing predation pressure on naticids. One difficulty in using repair frequency as a proxy for crushing predation intensity (as the authors did note) is that repair scars represent failed attacks. Repair frequency is a function of both attack frequency and attack success (or, from the prey's perspective, the relative defendability of the prey) (Vermeij, 1987; Leighton, 2002; Alexander and Dietl, 2003). Higher repair frequency may represent an increase in attack frequency, leading to an increase in total mortality due to crushing. However, higher repair frequencies may also be attributed to decreases in attack success, which would lead to a decrease in crushing mortality. If a trophic cascade is in effect, a decrease in crushing mortality on naticids would be expected to lead to increased drilling predation. Determining whether repairs are driven by attack frequency or attack success is key to using repair frequency to interpret crushing mortality, and in the present case, to evaluating the presence and possible effects of a trophic cascade.

A more direct measure of predation intensity is evidence of successful attacks in the form of crushed or (in the case of gastropod prey) peeled shells. When predation is successful, the gastropod is unable to repair its shell. It is generally considered difficult to distinguish predatory shell damage from taphonomic damage (Alexander and Dietl, 2003; Zuschin et al., 2003), causing many to rely on repair scars as evidence for crushing predation. However, researchers have consistently found that predatory damage can be distinguished from taphonomic damage (Oji et al., 2003; Kosloski, 2011). Stafford and Leighton (2011; in review) found that certain types of damage to the gastropod shell aperture are consistently attributable to crushing predation. Furthermore, experimental evidence supports such aperture damage as a sign of durophagous predation (see Stafford et al. (in review) and references therein).

Mondal et al. (2014) examined repair frequency and crushing mortality together, and determined that the use of both metrics greatly increases the interpretive power of predation studies. Attack frequency and the frequency of success are both important in exploring how predation influences the ecology and evolution of organisms. By assessing successful and unsuccessful predation, both crushing and drilling, we are best equipped to detect and interpret trophic cascades in fossil assemblages. In the present study, we used the abundant and diverse gastropod assemblage of the Miocene St. Mary's Formation of Maryland to examine the relationship between repair frequency and crushing mortality and to seek further evidence of TMII''s in ancient communities. The assemblages of the St. Mary's Formation contain a suite of drilling naticid gastropods, multiple species of gastropod prey, and crushing crabs similar to those found in modern shallow marine environments (Rathbun, 1935). These organisms form a trophic chain, from crabs to naticids to other mollusks. We approached the crab-naticid interaction, crushing predation, through repair frequency and the frequency of unrepaired predatory aperture damage. The naticid-mollusk interaction is represented by predatory drillhole frequency.

If aperture damage correlates positively with repairs, this suggests repair frequency is a direct proxy for attack frequency and mortality in the present study. If, on the other hand, they do not correlate, variation in repair frequency is likely a result of variation in attack success or failure; alternatively, it may be that taphonomic damage has masked the true signal of predatory damage. The system is further complicated by the fact that naticids are cannibalistic. If a trophic cascade is in effect, an increase in crushing predation may decrease cannibalistic activity, as is predicted with other prey gastropods; or, if cannibalism is a response to limited access to other prey, it may increase under increased crushing predation.

If TMIIs were at play in this trophic chain, increases in crushing predation intensity (as measured by unrepaired aperture damage or by repair frequency) should correlate with decreases in drilling frequency (and/or decreases in drilling success as measured by complete versus incomplete drillholes). If there is no relationship, or even a positive correlation, between crushing predation and drilling, it suggests that TMIIs had little or no effect on the trophic chain, or that any such effect was masked by other ecological factors.

MATERIALS AND METHODS

Geological Setting

Fossil material was collected from two localities in the St. Mary’s Formation, part of the Miocene Chesapeake Group, on the western shore of Chesapeake Bay (38.35° N, 76.41° W) (Figure 6-1). The St. Mary’s Formation differs from other Chesapeake Group units in being gastropod-dominated, rather than bivalve-dominated.

At one locality, Little Cove Point, the St. Mary’s Formation consists of alternating mud and sands (Kidwell, 1997), identified as the informal Shattucks molluscan zone 22, approximately 11 million years in age (Kidwell, 1997; Petuch and Drolshagen, 2010). Much of the St. Mary’s rock is well bioturbated, indicating an original soft substrate (a point supported by the relative paucity of epibenthic invertebrate fossils compared with other Chesapeake Group units) (Kidwell, 1997). An abundance of well-preserved gastropods and bivalves are found in two thick beds of coquina sand, as well as in thinner sandy intervals among much less fossiliferous muds. Kidwell (1997) noted that while the assemblage shows little signs of extensive reworking or time averaging (unlike in other exposures of the St. Mary’s Formation), the fauna suggests a muddier substrate than the coquina-sand in which it is found; thus, the fauna was likely transported from a nearby muddy habitat (Kidwell, 1997).

The second locality, Windmill Point, represents a stratigraphically higher portion of the St. Mary’s Formation, in Shattuck zone 24 (Petuch and Drolshagen, 2010). The paleoenvironment represented by the Windmill Point sands was more deep and open-shelfal than Little Cove Point, deposited during a warmer climatic interval hosting a similar, but slightly more tropical fauna (Petuch and Drolshagen, 2010). Figure 6-2 shows our stratigraphic sections.

Sampling

We collected samples from the cliff exposure at Little Cove Point, dividing the section into five fossiliferous beds (Figure 6-2). We collected samples from identifiable slump blocks to avoid damaging the intact cliffs. Samples were only collected from large slump blocks that could be easily correlated with the cliff stratigraphy. From each bed, we collected at least one 1-gallon bag of bulk sediment, using a trowel to dislodge the sediment from the slump block. We focused on obviously fossiliferous patches for each sample, but made no effort to collect particular taxa or specimens of particular size or preservation.

At Windmill Point, the sampling protocol was the same, except that the three 1-gallon samples were collected directly from the very low (~ 1 m) cliff exposure. The Windmill Point samples were treated as one bed.

In the laboratory, material larger than 3 mm mesh size was separated for use in the present study. From the > 3 mm fraction, identifiable gastropod, bivalve, and other fossils were sorted, regardless of preservation.

Study specimens

Four gastropod groups, of varying taxonomic level, were chosen for further analysis, based on abundance and on potential for predation metrics. This meant that A) the group had to be abundant enough to provide robust sample sizes in most of the samples, B) the specimens had to be easily and accurately countable (very high-spired gastropods tended to break into several pieces, making accurate counts difficult), and C) the group had to be well-preserved enough that predation metrics (drilling frequency and repair frequency) could be observed and recorded from the specimens. Four groups fit these criteria.

Small naticids (at least 3 mm, and no larger than 10 mm in diameter), in the genera *Euspirella* and *Neverita*, were grouped together into a single category, “naticids” (Figure 6-3a). The “naticid” category by far was dominated by *Euspirella* of undetermined species; in many cases, the naticid samples were essentially *Euspirella* samples. *Neverita* specimens were included due to the similar size range to *Euspirella* and the occasional difficulty in distinguishing the two genera. Based on the size of the naticid drillholes observed on the small gastropods (and bivalves) in the samples, it is likely that the small *Euspirella* and *Neverita* were responsible for this drilling predation. Naticid specimens larger than 10mm diameter were eliminated from the analysis, due to their rarity and the likelihood that they favored larger prey than the gastropods used in this study.

Ilyanassa peralta was the most abundant taxon in the collection. *I. peralta* is a small (3 mm – 13 mm) nassariid, whelk-shaped with a basket-weave ornament of spiral and axial cords (Figure 6-3b). Cursory inspection of specimens showed that they tended to be very well preserved and often drilled. The intricate shell ornament made repair scars relatively easy to identify.

Mitrella communis [aka *Astyris communis*, aka *Columbella communis*] [size range 3 mm – 10 mm] is a small columbellid gastropod, teardrop-shaped with a smooth, unornamented surface. The outer lip of the aperture is slightly flared and weakly toothed (Figure 6-3c). Specimens were well-preserved but infrequently drilled.

Microturrids [size range 3 mm – 10 mm](Figure 6-3d) comprised all specimens within the family Turridae under approximately 10 mm shell height, and not clearly belonging to other larger-sized turrid taxa. The vast majority of specimens appeared to belong to the genus *Mangelia*, based on descriptions and plates in Gibson (1962), but identification was difficult due to the specimens' small size and mutable shell characters. The microturrids all bore prominent sculpture, ranging from smooth knobs to fine threads and beads. The specimens were frequently drilled, but their small size and variable preservation made repair scars impossible to assess accurately.

Another taxon, *Bulliopsis marylandica*, was present in the assemblages collected for this study. *B. marylandica* is the subject of a separate study examining crushing and drilling predation (Stafford and Leighton, in review). *B. marylandica*, a buccinid gastropod of about 20 mm height, is much larger than the gastropods examined in the present study and was not abundant enough to examine at as fine a stratigraphic resolution as that employed in the present study. It is unlikely that *B. marylandica* had direct trophic interactions with the gastropods in this study.

Predatory crabs were present in the assemblage: fragments of molariform chelae were found in many samples, although the specimens were too fragmentary and rare to identify and count. Major crushing predators that have been identified in the Maryland Miocene include portunid, xanthid, and cancrid crabs, as well as stomatopods (Rathbun, 1935).

Predation metrics

For each of the four gastropod groups, four predation metrics were calculated.

1. Drilling frequency (DF) was calculated as the number of specimens bearing a complete naticid drillhole, divided by the total number of specimens on which drilling status could be assessed. Changes in drilling frequency may indicate how much time naticids were able to allot to foraging; under increased crushing predation pressure, naticids may reduce their foraging in order to avoid crushers.

2. Drilling success frequency (DS), calculated as the number of complete drillholes divided by the total number of attempted drillholes (complete and incomplete). Success frequency indicates whether naticids were frequently interrupted during drilling or otherwise unable to complete drillholes. Low DS is one expected outcome of increased crushing predation on drilling predators.

3. Repair frequency (RF) was calculated as the number of specimens bearing a repair scar on the body whorl, divided by the total number of specimens on which such repairs could be assessed (due to differences in the number and preservation of exposed whorls, only repairs on the body whorl were counted). Repair frequency on naticids is one potential indication of crushing predation pressure; however, it may also be an indication of prey fitness, in that better-defended prey are more likely to survive attacks and repair the damage. RF was measured on naticids to assess differences in predation and connect those to possible differences in drilling frequency, due to TMIIs. We also measured RF for the other gastropod prey groups, to see if differences in crushing predation were consistent for all prey among the sampled beds.

4. Crushing frequency (CF) is the proportion of individuals bearing unrepaired predatory damage. As with repair frequency, crushing frequencies were calculated for naticids (to assess TMIIs) and for the other gastropod groups, to see if there were consistent trends in predation among the samples. CF was calculated one of two ways, depending on the prey group. For *Ilyanassa peralta*, shell crushing was assessed using damage categories determined to be predatory based on Vermeij Crushing Analysis by Stafford and Leighton (2011, in review). For naticids, *Mitrella communis*, and microturrids, probable predatory shell peels were assessed individually on each shell, because the specimens were either insufficiently preserved or insufficiently drilled (*M. communis*) to perform VCA (see below).

Repair frequency and crushing frequency were used in concert to assess crushing predation because both methods have strengths and weaknesses. Repair frequency is relatively easy to obtain, but the interpretation of repair frequency is ambiguous (i.e., whether RF is driven by attack frequency or by prey defendability). Crushing frequency is unambiguous (unrepaired damage means the prey died before repairing the shell), but crushing damage is more difficult to detect with certainty on individual shells. Thus, we used both metrics to A) examine the relationship between RF and CF and to B) obtain as much information as possible pertaining to crushing predation intensity. Repair frequency and crushing frequency were also combined as repair+crushing frequency (R + C), calculated as the number of specimens bearing a repair and/or crushing damage, divided by the total number of specimens. If repairs and lethal crushing are directly related, this combined metric may give more robust data for comparison with drilling frequencies.

Vermeij Crushing Analysis

Vermeij Crushing Analysis (VCA; Stafford and Leighton, 2011, in review) estimates crushing predation on gastropod shells by accounting for and eliminating the effects of taphonomy (Vermeij, 1982). In the present study, VCA was performed on *Ilyanassa peralta* to determine crushing frequency and to compare it with repair frequency. *I. peralta* was by far the most abundant, well-preserved, frequently drilled taxon in the assemblage. The other prey groups were either not abundant enough, or not frequently enough drilled, to apply VCA (see Stafford and Leighton, in review).

Multiple categories of shell damage are compared between shells bearing complete naticid drillholes (drilled shells) and shell without drillholes (undrilled shells). Because drilled shells were most likely killed by a naticid predator, any fragmentation to those shells is taphonomic (Vermeij, 1982; Stafford and Leighton, 2011, in review). This taphonomic damage is quantified, then subtracted from the fragmentation seen on the undrilled shells. Any remaining fragmentation should be due to crushing predation, not taphonomy.

VCA was performed as in Stafford and Leighton (in review), using the damage categories presented in that paper. Certain categories are not expected to result from crushing predation, and act as controls. The remaining categories previously have been attributed to crushing predation (using VCA (Stafford, and Leighton, 2011, in review) and experimentally (see Stafford et al. (in review) for list of references)).

The damaged-undamaged occurrences of each category for drilled and undrilled shells were compared for each sample of *I. peralta* using Fisher's exact test. If damage due to crushing predation can be separated from taphonomic damage in the assemblage, damage frequencies will be greater among undrilled shells. This difference will represent the frequency of crushing mortality in the assemblage.

Statistical Analyses

For each gastropod group, we compared repair frequency with the frequency of unrepaired crushing damage (based on visual inspection for peels, or on damage associated with predation, by VCA) using Pearson's product-moment correlation. Although the number of samples is small enough that a statistically significant result is less likely, the direction of the correlation is still useful. A positive correlation would indicate that repair frequency is tracking crushing predation attacks and mortality, whereas a negative correlation would suggest that repairs are driven more by the success or failure of the predators.

To detect trophic cascade effects, we compared predation on naticids with drilling frequencies on all four gastropod groups (including naticids themselves, to assess any effect of crushing predation on cannibalistic behavior) using Pearson's product-moment correlation. Predation on naticids was represented four ways: as repair frequency, as crushing frequency, as repair+crushing frequency, and as repair + crushing + drilling frequency (i.e., the frequency of specimens bearing at least one type of predatory damage, including cannibalistic drillholes).

We also compared the frequencies among the gastropod groups for repairs, crushing, and drilling, to see whether they tended to vary predictably among the sampled beds.

RESULTS

Four of the sampled beds (C, D, E, and W) yielded sufficient sample sizes to to calculate valid predation metrics.

There were no consistent trends in drilling frequency among the four gastropod groups, although cannibalism (drilling frequency on naticids) increased steadily throughout the four sampled beds included in the analysis (Figure 6-4). Drilling success frequencies were consistently very high, ranging from 0.95 – 1 (Table 6-1).

There were no consistent trends in repair frequency or crushing frequency among the four gastropod groups through the four analyzed samples (Figures 6-5 and 6-6).

The associations between repair frequency and crushing frequency were mostly negative, but nonsignificant (Table 6-2, Figure 6-7).

The presence of a trophic cascade was tested using crushing frequency and repair + crushing frequency versus the drilling frequencies of the four prey groups. Among these comparisons, most of the correlations were positive, and none were significant at $p = 0.05$ (Table 6-3, Figure 6-8). Naticid repair + crushing frequency was positively correlated ($r = 0.93$) with naticid drilling frequency at p = 0.069 (Table 6-3).

Ilyanassa peralta drilling frequency was significantly negatively correlated with *Mitrella communis* drilling frequency (r = -0.96, p = 0.042) (Figure 6-4). Naticid crushing frequency was significantly negatively correlated with microturrid crushing frequency (r = -0.99, p = 0.013) (Figure 6-6). There were no other significant correlations among drilling frequencies, among repair frequencies, or among crushing frequencies.

DISCUSSION

The relationship between repair frequency and crushing frequency is negative, though nonsignificant, for all four gastropod groups. With only four samples included in the analysis, a very strong relationship would be necessary to produce significant results; however, inspection of the graph (Figure 6-7) supports the interpretation that the two metrics are inversely related. This may be evidence that among these species, repair frequency is driven by *success* of attacks, not frequency of attacks. When prey are better defended (or predators less capable), more attacks fail, producing higher repair frequency and lower mortality. This in itself affirms the need to address predation mortality directly, rather than relying exclusively on repair frequency as a proxy.

The relationship between crushing predation and drilling suggests that the interactions between crushing crabs and naticids were weak. Considering crushing frequency alone (since repair frequency appears to be inversely related to mortality), the correlations with drilling were weak and nonsignificant. While three of the four correlations were negative (the relationship that would be expected if crushing predation was suppressing drilling predation), inspection of the graph (Figure 6-8) suggests no discernable pattern. Thus, it appears that crushing predation did not suppress drilling activity by naticids.

The weak negative relationships seen between crushing on naticids and drilling frequency could reflect a stronger relationship masked by taphonomy. The Vermeij Crushing Analysis results for *Ilyanassa peralta* may indicate that unrepaired, lethal damage has been obliterated by subsequent taphonomic damage. If this is the case, the amplitude of variation in crushing mortality may be dampened in our present crushing frequency calculations. Also, crushing predators that are very powerful relative to their prey are capable of destroying the prey shell, leaving no identifiable fragments. Such destruction could “hide” the evidence of crushing mortality in an assemblage. However, the frequent repair scars on the gastropod groups show that weaker predators (those who peel the shell aperture, rather than completely crush the shell) did attack relatively frequently.

The strongest evidence that crushing predation was not suppressing naticid drilling behavior is the extremely low occurrence of incomplete drillholes. If encounters with crushing crabs affected naticids' ability to drill, naticids would forage less (resulting in low overall drilling frequencies) and/or abandon partially-drilled prey when interrupted by crushing predators (resulting in high occurrences of incomplete drillholes). Neither of these predictions is borne out in the data (Table 6-1). Drilling success frequencies varied from 95% to 100%, showing that naticids rarely abandoned their prey.

If, indeed, there was no appreciable pattern between crushing and drilling in the system, we may ask why this was. How did naticid drilling escape the negative effects of crushing predation?

Crushing predation on naticids may have been too low to hinder naticid drilling. Estimated crushing frequencies on naticids were quite low (ranging from 0.03 – 0.14), as were repair frequencies (0.00 – 0.15) (Table 6-1), suggesting that crushing attacks on naticids were both infrequent and survivable.

The low frequency of crushing attacks on naticids may imply that crabs preferred other types of prey, or that the encounter rate between crabs and naticids was low (these scenarios are not mutually exclusive). Naticids forage in soft substrate, often on mobile prey (Carriker and Yochelson, 1968). Foraging semi-infaunally to infaunally may limit naticids' exposure to crushing predators; it may even provide refuge against epifaunal predators. Naticids may also be able to escape crushers by burrowing deeper into the substrate, without abandoning their prey. The naticids in this study may have been difficult for crushing crabs to catch, leading the crabs to focus on easier prey, such as sedentary bivalves such as *Spisula*.

Gonnerman et al. (2011, in a conference abstract) reported a very slight reduction in the average total prey consumed by *Neverita duplicata* in the presence of the predatory crab *Callinectes sapidus*, compared with *Neverita duplicata* in a control treatment, suggesting that naticid feeding was suppressed by the predators. However, the sample sizes were small and drilling success frequency was not reported. The presence of the predator may also have suppressed cannibalism by the larger naticids. In the present study, we found no discernable relationship between crushing predation and cannibalistic drilling. More work is required to determine how predation affects naticid drilling behavior, success frequency, and prey preference and cannibalism.

The counterpart to the weak crab-naticid interaction is the strong naticid-mollusk relationship. The low incidence of crushing predation may have allowed the naticids to sustain high drilling frequencies and drilling success throughout the assemblages. Throughout the fossil record of naticids, drilling frequencies and success frequencies vary greatly in different assemblages (e.g., Kelley, 1988; Kelly and Hansen, 1996). It would be of immense value to assess crushing predation among these assemblages to confirm whether suppressed drilling activity is a result of more intense crushing predation.

CONCLUSION

Among four groups of gastropods in the Miocene St. Mary's Formation, there was a weak but negative relationship between crushing predation frequency and crushing repair frequency, suggesting that repair frequency was a factor of predator ability and prey defense, rather than attack frequency. Crushing and repair frequencies on naticids were low. In conjunction with both high naticid drilling frequencies and high drilling success frequencies, this suggests that crushing predation was too low to suppress naticid drilling behavior in these assemblages. Note that this result does not necessarily refute the existence of a trophic cascade. A cascade indicates that the interaction between a high and intermediate trophic level will influence the strength of the interaction between that intermediate trophic level and a still lower level. A strong interaction at the higher level will produce a weaker interaction at the lower level (e.g., intense crushing predation will lead to weakened drilling predation) but the opposite relationship is also possible -- in the present study, a weak interaction at the higher level (little crushing predation) may have allowed for a strong interaction at the lower level (high drilling frequency and success). Examinations of crushing predation on naticids in assemblages with low drilling predation (and/or high incidences of incomplete drillholes) may further support this interpretation of the role of crushing predation in regulating naticid drilling behavior.

FIGURES

Figure 6-1. Map of the study region (star) in Maryland, on the western shore of Chesapeake Bay in the mid-Atlantic region of the United States.

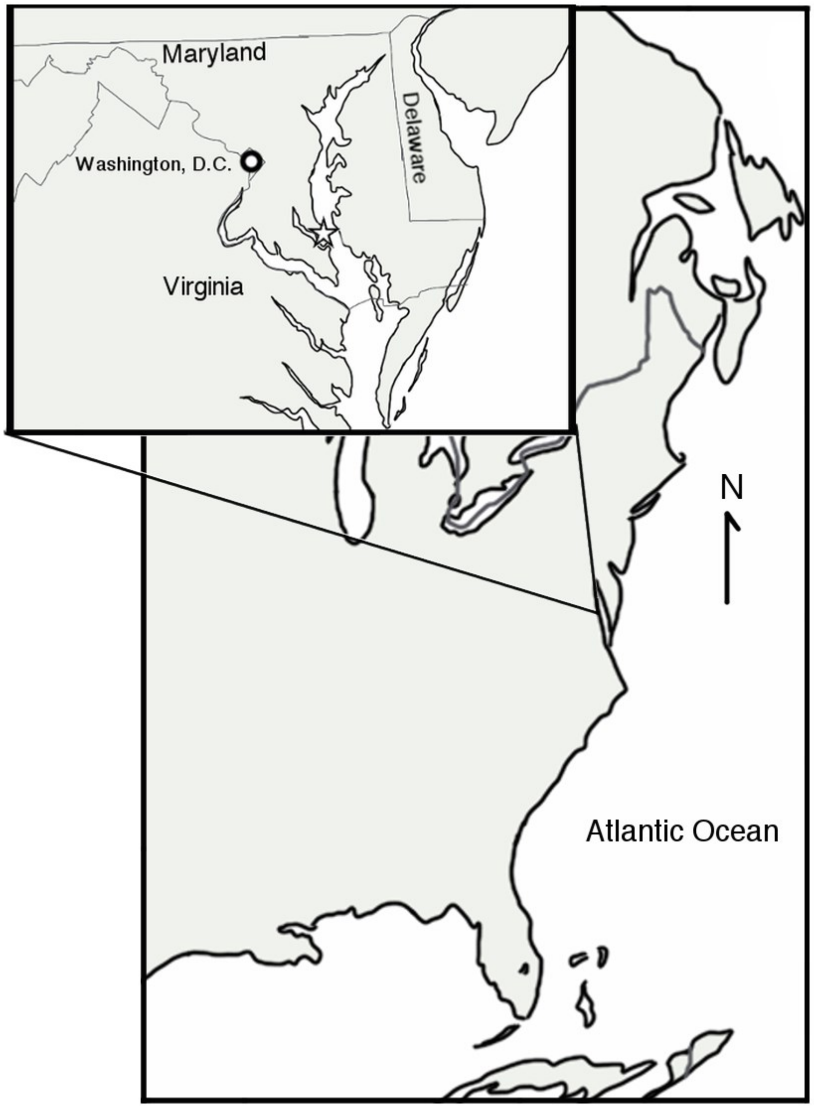


Figure 6-2. A. Stratigraphic column showing the sampled intervals at Little Cove Point and Windmill Point. Depicted lithologies range from clay to sand. B. Photograph of the Little Cove Point exposure. The vertical scale of the LCP photograph approximates that of the LCP stratigraphic column.

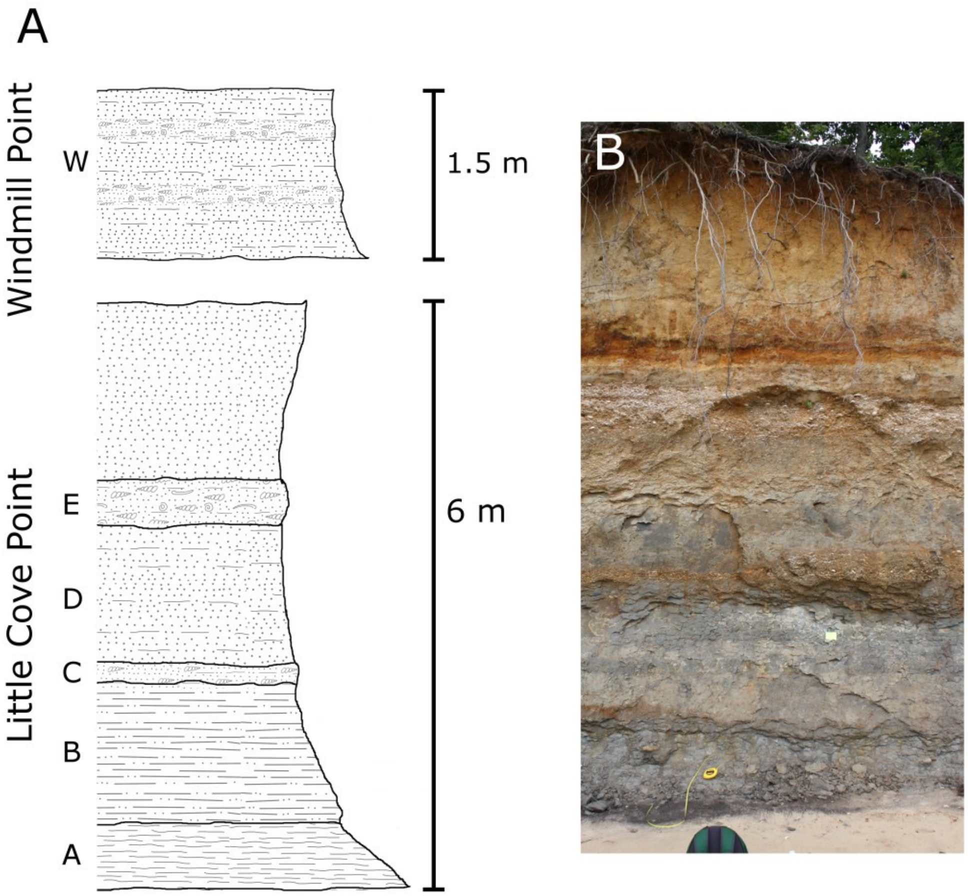


Figure 6-3. The four gastropod groups used in this study. All scale bars equal 1 cm. A. Naticids, primarily *Euspirella*. B. *Ilyanassa peralta*. C. Microturrids. D. *Mitrella communis*.

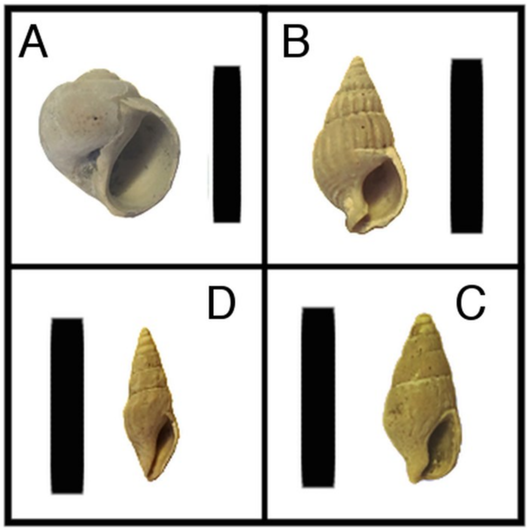


Figure 6-4. Drilling frequencies on each gastropod group through the stratigraphic section.

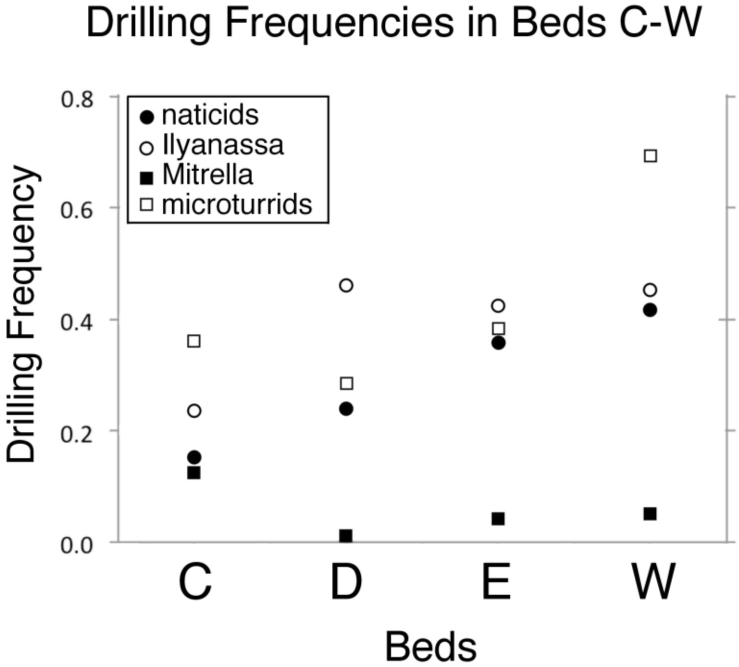


Figure 6-5. Repair frequencies on each gastropod group throughout the stratigraphic section.

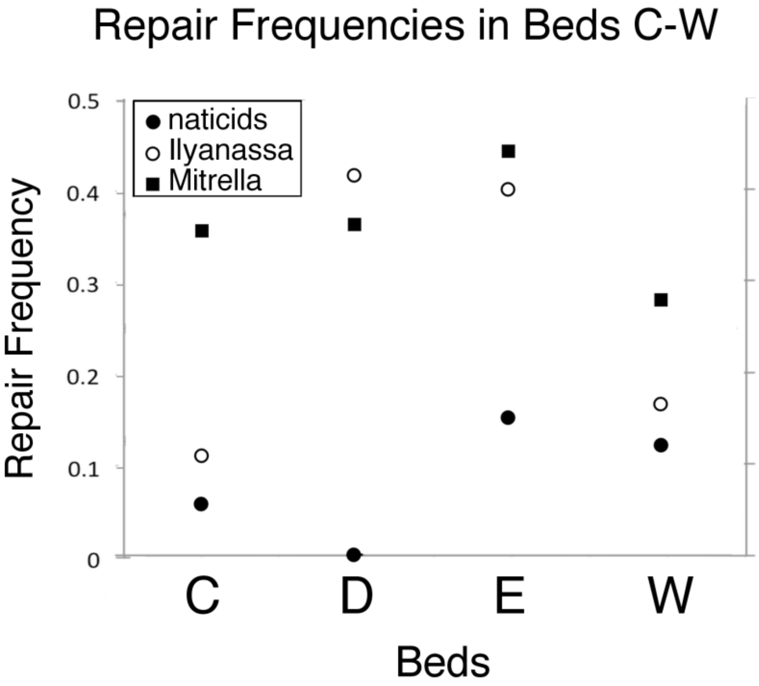


Figure 6-6. Crushing frequencies on each gastropod group throughout the stratigraphic section.

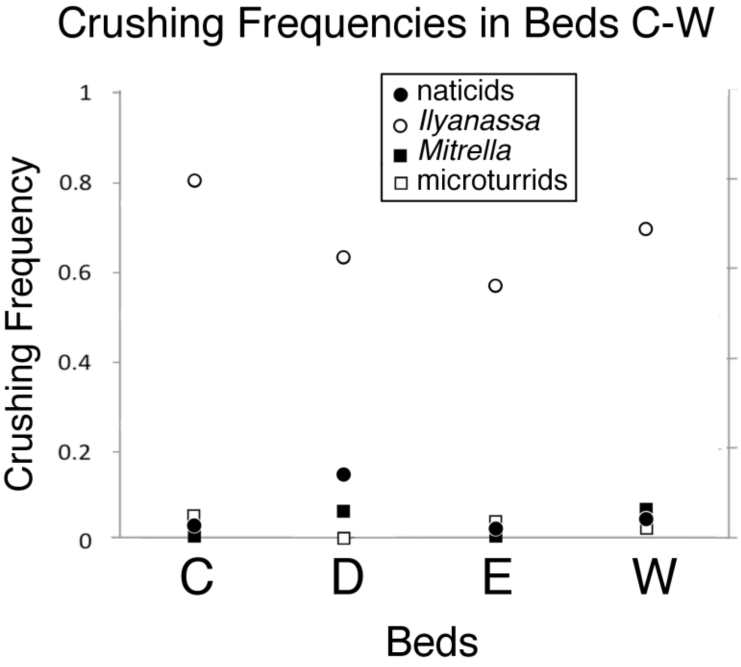


Figure 6-7. Repair frequency versus crushing frequency for three of the four gastropod groups examined.

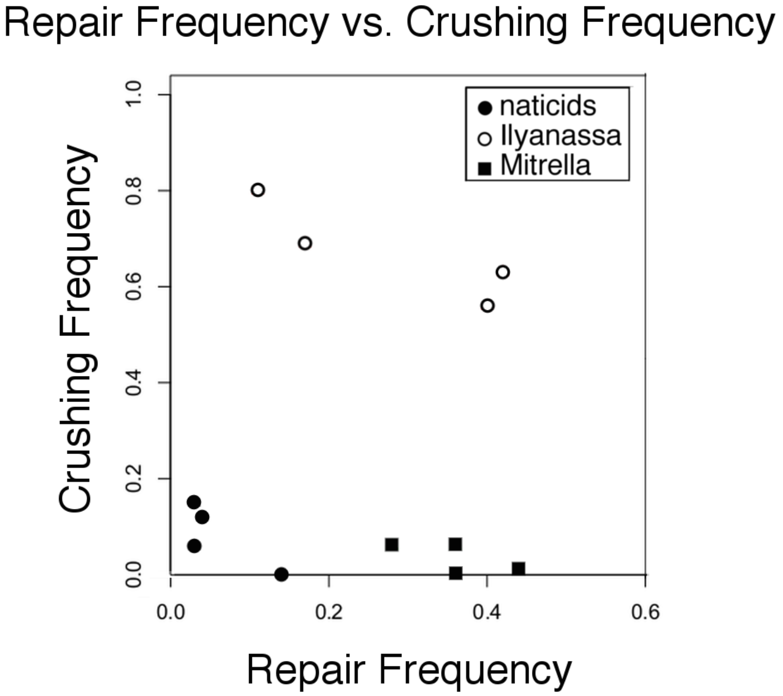
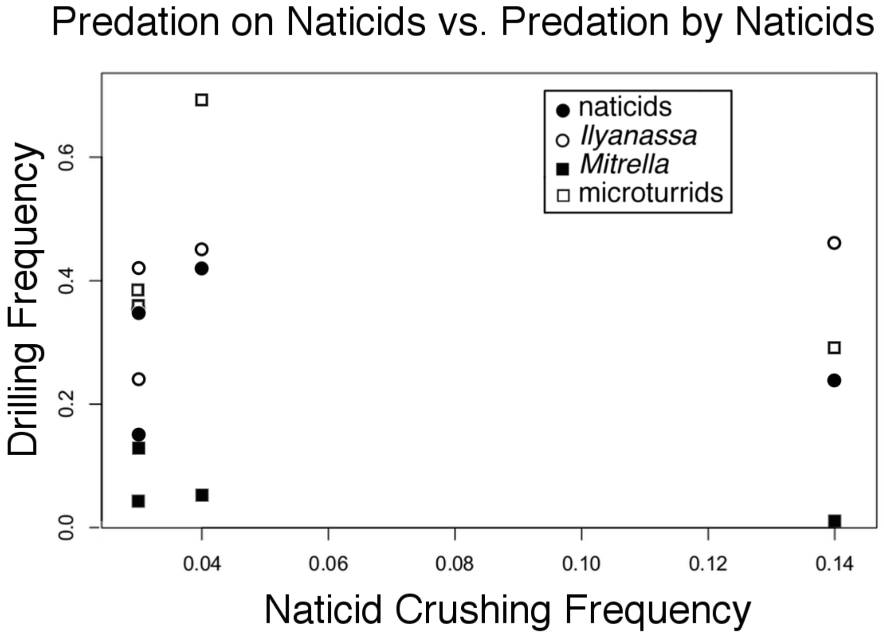


Figure 6-8. Comparison between crushing frequency on naticids and drilling frequency by naticids on the four gastropod groups. Note that drilling predation on naticids represents confamilial (or even conspecific) cannibalism.



TABLES

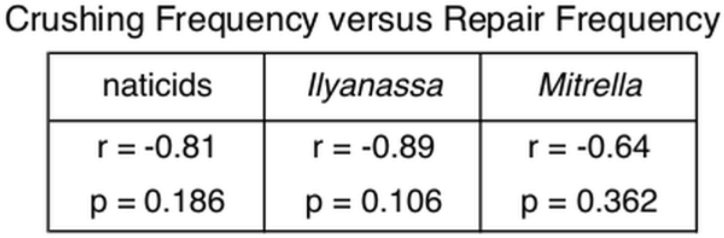
Table 6-1. Predation metrics, organized by bed and by gastropod group. Due to small size and poorer preservation, repair frequency was not calculated for the microturrids.

Predation Metrics by Bed and Gastropod Group

	Abundances				Drilling Frequencies				Drilling Success Frequencies			
Bed	naticids	*Ilyanassa*	*Mitrella*	microturrids	naticids	*Ilyanassa*	*Mitrella*	microturrids	naticids	*Ilyanassa*	*Mitrella*	microturrids
W	567	407	183	131	0.42	0.45	0.05	0.69	1	1	1	1
E	313	892	202	138	0.36	0.42	0.04	0.38	1	0.99	1	0.95
D	197	660	137	51	0.24	0.46	0.01	0.29	1	1	1	1
C	86	164	15	82	0.15	0.24	0.13	0.36	1	1	1	1

	Repair Frequencies			Crushing Frequencies			
Bed	naticids	*Ilyanassa*	*Mitrella*	naticids	*Ilyanassa*	*Mitrella*	microturrids
W	0.12	0.17	0.28	0.04	0.69	0.06	0.03
E	0.15	0.40	0.44	0.03	0.56	0.01	0.04
D	0.00	0.42	0.36	0.14	0.63	0.06	0.00
C	0.06	0.11	0.36	0.03	0.80	0.00	0.04

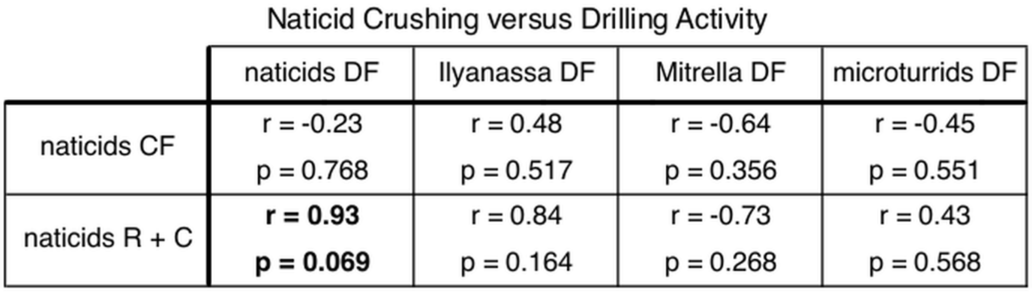
Table 6-2. Crushing frequency versus repair frequency for three of the gastropods in this study. Crushing frequency was determined by counting probable predatory peels on naticids, *Mitrella*. Crushing frequency was determined using Vermeij Crushing Analysis on *Ilyanassa*. Due to small size and poorer preservation, repair frequency was not calculated for the microturrids. See Figure 6-7 for data.



Crushing Frequency versus Repair Frequency

naticids	*Ilyanassa*	*Mitrella*
r = -0.81 p = 0.186	r = -0.89 p = 0.106	r = -0.64 p = 0.362

Table 6-3. Pearson product-moment correlations between crushing predation on naticids and drilling predation on the four types of gastropods. CF = crushing frequency. CF was determined by counting probable predatory peels on naticids, *Mitrella*, and microturrids. CF was determined using Vermeij Crushing Analysis on *Ilyanassa*. R + C = frequency of specimens bearing a repair scar and/or predatory peel. None of the correlations were significant at $p < 0.05$, but one correlation was marginally significant at $p = 0.069$, indicated in bold. See Figure 6-8 for data.



Naticid Crushing versus Drilling Activity

	naticids DF	Ilyanassa DF	Mitrella DF	microturrids DF
naticids CF	r = -0.23 p = 0.768	r = 0.48 p = 0.517	r = -0.64 p = 0.356	r = -0.45 p = 0.551
naticids R + C	**r = 0.93** **p = 0.069**	r = 0.84 p = 0.164	r = -0.73 p = 0.268	r = 0.43 p = 0.568

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CHAPTER 7
CONCLUSIONS

Despite the destructive nature of crushing predation on gastropod shells, there are many viable ways to approach questions of crushing predation in modern and fossil environments. Quantifying the interactions among gastropods, hermit crabs, and their shared predators may illuminate how predation influences the ecology and evolution of these shelled prey.

Crushing predation can be identified in gastropod shell assemblages in three ways. Most directly, individual instances of peeling predation are recognizable on shells due to the highly stereotyped damage left on the shell (Chapter 2). As a trace fossil, *Caedichnus spiralis*, peeled shells provide information not just about the fate of the prey, but also the identity, size, and degree of specialization of the predator. In particular, decapod crustaceans are the most likely culprits in cases of peeling damage, but other crustaceans, mammals such as rats, and even molluscivorous birds may produce peel-like damage. Peeling predation in particular, compared with other crushing techniques, is especially likely to fail, allowing for the differential mortality that drives the evolution of antipredatory behaviors and morphological features (Vermeij, 1982a). Thus, the identification and interpretation of *C. spiralis* is an important part of predation research.

Much predatory damage is far more destructive than shell peeling, and is thus less likely to leave easily identifiable evidence. Although repair frequency (a measure of unsuccessful predatory attacks) tends to be easily accessible in gastropod shell assemblages, its relationship with predation mortality is ambiguous. Chapter 5 explored Vermeij Crushing Analysis (VCA), building upon the work of Vermeij (1982b) and Stafford and Leighton (2011). Despite differences in geography, age, and taxon, the predation mortality and patterns among modern and fossil gastropod shells were remarkably similar, with aperture damage greater than 90° being almost certainly attributable to predation. These findings are congruent with the definition of *Caedichnus* put forth in Chapter 2. The main drawback of VCA is that it requires a gastropod assemblage to consist of a significant number of drilled shells in order to establish a taphonomic baseline against which to assess crushing damage. The congruence between the VCA results and *Caedichnus* suggests the possibility of identifying individual instances of crushing predation in shell assemblages, bypassing the need for a taphonomic baseline from drilled shells.

The other most accessible type of indirect evidence for crushing predation is shell repair, where individual prey survive attacks and regrow damaged shell. Shell repair frequency can be used to assess how often prey survived attack, but it does not necessarily give information about how frequent attacks are in general. Thus, the mortality due to crushing predation cannot necessarily be inferred from repair frequency. In a modern setting, shell repair frequency was compared with predation mortality to determine whether repair frequency is a valid proxy for mortality (Chapter 3). In this study, repair frequency was found to vary directly with the predation intensity, suggesting that repairs can be used to infer mortality.

However, the opposite relationship was found when examining repairs and successful predation in a fossil environment (Chapter 6). Chapter 6 applied VCA and repair frequency, along with predatory drilling frequency, to examine predation at multiple trophic levels in gastropod material from the Miocene St. Mary's Formation. Results showed that crushing predation did not have a strong impact on naticid drilling predation; crushing predation pressure was not intense enough to reduce naticid drilling frequency or drilling success (both of which were high). Additionally, there was not a strong relationship between repair frequency and crushing frequency (as measured by VCA and crushing traces). This suggests that in this community, variation in repair frequency was not a result of variation in predatory attack frequency; it is more likely that repair frequency was driven by predator success. This contrasts with the findings of Chapter 3 (that repairs were directly related to mortality). The most important message taken from this contrast is that studies on predation should utilize as many predation metrics as possible: it is not possible to know *a priori* how to interpret repair frequency. While each metric provides valuable information in its own right, the true value of predation data lies in the potential to illustrate the larger, complex picture of predatory interactions.

Habitation by hermit crabs adds another variable to an already complex system. Chapter 4 approached the issue of predation on hermit crabs, a potentially confounding factor in the predation patterns gleaned from gastropod shell assemblages. There was no discernible preference by predatory crabs for snail or hermit crab prey. On the other hand, there was a significant difference in handling time, with hermit crab prey taking less time to crush and consume. This may indicate differences in the ease of crushing hermit crab shells and/or differences in the amount of edible flesh available for consumption.

The issue of hermit crab habitation was also addressed in Chapter 5, while performing VCA. Pagurized shells (those bearing bioerosive traces associated with hermit crab habitation) were removed from the analysis and were analyzed separately to determine whether hermit crabs experienced more, less, or the same amount of predation as gastropods. As found in Stafford and Leighton (2011), pagurized shells bore less crushing predation associated damage than nonpagurized shells, suggesting that the inclusion of pagurized shells might lead to underestimates, rather than overestimates, of crushing predation on gastropod shell assemblages.

Taken together, the studies in this dissertation illuminate the hazy border between what is possible and impossible in the study of predation on shelled prey. It is likely that data concerning crushing predation are present in gastropod assemblages; it is less clear how to accurately extract and analyze the data. Research expanding upon the findings of these chapters will clarify these unanswered questions and lead to a deeper understanding of the relationship between predators, prey, and the world they inhabit.

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