Investigating Predation in the Fossil Record: Modern Analogs

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Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

In

Geosciences

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February 3rd, 2012
Blacksburg VA

Keywords: Predation Traces, Toxicity, Durophagy, Morphology

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ABSTRACT

Predation is considered a powerful ecological force influencing community structure, diversity, and abundance. Paleoecology offers a unique perspective, allowing us to examine ecological processes such as predation over evolutionary timescales. The three studies summarized below include two case studies testing the role of predation in evolution and one method-oriented project, which explores new tools with which to examine predator-prey interactions in the fossil record. Considering the importance of community interactions in the current global biodiversity crisis, understanding ecological and evolutionary dimensions of predation is critical to conservation biology and ecology, as predators are thought to play a vital role in maintaining ecosystem health and biodiversity.

Predation has been dismissed as a causal mechanism for some major prey groups. For example, the evolutionary decline and cryptic or antitropical distribution of brachiopods is often explained as due to the potentially low energetic value and suspected non-palatability or toxicity of brachiopod tissues. Here we demonstrate that multiple invertebrate marine predators (crustaceans, echinoderms, and gastropods) are willing and able to consume brachiopods, and that predation pressure on the living brachiopod population may be consequential. Examination of the fossil record is consistent with this interpretation: evidence for drilling and repair of brachiopod shells is found throughout the fossil record in multiple orders. This suggests that although brachiopods may be unwanted prey in the presence of energetically more desirable targets, they do appear to be edible and are subject to intense predator-prey interactions.

Limpets are important prey for some crab species, yet little is known about the role of durophagy in the evolution of the limpet shell. Feeding trials using three common species of Pacific Northwest limpets (Lottia digitalis, L. pelta and Tectura scutum) were conducted to assess how different shell morphologies affect mortality and handling time. We predicted that large size, shell ornament, and low-spires would result in either increased survivorship,

and/or longer handling times. Contrary to our expectation that ridges resist predation, individuals with smooth morphologies experienced significantly lower mortality, as did those with low-spires. As species possessing high-spires and ridges typically occur high in the intertidal where predation risk due to crabs is relatively low, these morphologies are likely adaptions to physical factors such as thermal stress.

One of the major caveats of using gastropod drill holes to assess predator-prey interactions in both the modern and the ancient is the correct identification of drill holes of predatory origin. By examining known predatory drill holes using environmental scanning electron microscopy, we aim to refine the development of a novel technique for augmenting their identification, and to explore the relationship between predator body size, predatory radula dentition, and radular microrasping marks observed on the shells of prey organisms. Electron micrographs were used to measure the spacing of microrasping marks produced by the radula, and the intercusp spacing of the radula dentition. A relationship between predator body size and microrasping marks makes it possible to infer predator size from these microtraces in both modern and fossil specimens, augmenting our ability to examine predator-prey interactions throughout the history of this important ecological interaction.

Proxies for predation intensity such as predation traces or antipredatory morphologies provide an invaluable method to examine predation in both modern communities, and the fossil record. Our understanding of the importance of predation in regulating biodiversity and in evolution will continue to grow with the development of new methodologies, and a comprehensive understanding of predatory defenses.

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DEDICATION

For Lindsey Leighton my academic father, mentor, and friend.

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CHAPTER 1

INTRODUCTION

Predation is considered an important force in many communities, influencing biodiversity and community structure on a variety of spatial and temporal scales (Paine 1966; MacArthur 1972; Vermeij 1977; Palmer 1979; Vermeij et al. 1980; Vermeij et al. 1981; Vermeij 1987; Hansen and Kelley 1995; Hoffmeister and Kowalewski 2001; Leighton 2002; Huntley and Kowalewski 2007). To evaluate the role of predation in evolution, however, we need effective proxies for predation pressure. For example, arguments that predation intensity should covary with biodiversity (e.g., Vermeij 1977; Signor and Brett 1984; Vermeij 1987) commonly utilize predation trace frequencies and prey defenses as proxies for predation intensity. Predation traces, such as drill holes and repair scars, are widely used proxies as they provide direct evidence of predator-prey interactions, and are commonly preserved in prey skeletons in the fossil record (Kowalewski and Kelley 2002). Increases in prey defenses (Vermeij 1977, 1983; Vermeij 1987) and shell armaments have also been used to argue for the importance of predation in regulating communities during periods of increased predation pressure in the mid-Paleozoic (Signor and Brett 1984), and Mesozoic (Vermeij 1977). Considering the utility of proxies for predation intensity, developing novel techniques for the identification of predation traces, and identifying antipredatory shell morphologies are important steps in understanding the role of predation as an evolutionary force. The chapters presented below focus on (1) the use of predation traces to assess brachiopod toxicity and predation pressure on both modern and ancient brachiopods, (2) assessment of limpet shell morphologies in terms of potential antipredatory adaptations, and (3) the development of novel techniques to identify drilling predation traces and extract ecological information from drill holes.

SUMMARY

Chapter one, "Does predation play a role in the decline of post-Paleozoic brachiopods? Re-visiting chemical defenses and palatability" is not yet submitted for publication, and the expected submittal date to the journal *Paleobiology* is February 2012. Predation has been put

forth as an important force in the post-Paleozoic decline in diversity and abundance of rhynchonelliform brachiopods. This study, therefore, aims to establish the potential for predation as a driving force in brachiopod evolution by refuting the commonly held belief that rhynchonelliform brachiopods are toxic. Here, we combine experimental, neontological, and paleontological data to assess brachiopods as viable prey to explore (1) the palatability and value of brachiopod prey to durophagous predators, and (2) the Phanerozoic record of predation based on a comprehensive survey of reported rhynchonelliform predation traces (repair scars and drill holes).

Chapter two, "The role of limpet shell morphology in resisting durophagous predation by adult cancrid crabs" is not yet published, and the expected submittal date to *The Journal of Experimental Marine Biology and Ecology* is March 2012. The study aims to identify antipredatory morphologies in limpet shells utilizing laboratory feeding trials. Although limpets are important prey for some crab species (Chapin 1968; Lowell 1986; Thompson et al. 2000; Cannicci et al. 2002; Silva et al. 2008; Silva et al. 2010), little is known about the role of durophagy in the evolution of the limpet shell, relative to spirally coiled gastropods. Some large-scale geographic trends in limpet morphology due to predation have, however, been observed: limpets in tropical regions have greater tenacities, better developed armor, and thicker shells due to increased durophagous predation (Lowell 1987; Vermeij 1987). The identification of additional antipredatory limpet shell morphologies, therefore, could prove useful to explore the role of predation in the spatial variation of limpet abundance and diversity. This study examines the vulnerability of three species of common Pacific Northwest limpets *Lottia digitalis*, *Lottia pelta*, and *Tectura scutum,* to durophagous predation by *Cancer productus*. Feeding trials were conducted to assess how different shell morphologies affect mortality and handling time with respect to: (a) prey size, (b) shell ornament, and (c) low-spires.

Chapter three, "The fidelity of microstructural drilling predation traces and gastropod radula morphology: paleoecological applications" is not yet published, and the expected submittal date to the journal *Palaios* is February 2012. One of the major caveats of using gastropod drill holes to assess predator-prey interactions in both the modern and the ancient is the correct identification of drill holes of predatory origin. By examining known predatory drill holes using

scanning electron microscopy, we aim to further our understanding of the relevance and utility of drilling predation microtraces in the identification of traces made by predation, and in extracting ecological information from drill holes. The characterization of radular rasp marks could be of particular importance in paleontological studies where the identity of the predator is often uncertain, or the predator population is not preserved in the assemblage. In addition, a relationship between predator body size and microrasping marks would facilitate the use of microtraces as a proxy for predator size, augmenting our ability to examine the history of this important ecological interaction.

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CHAPTER 2

DOES PREDATION PLAY A ROLE IN THE DECLINE OF POST-PALEOZOIC BRACHIOPODS? RE-VISITING CHEMICAL DEFENSES AND PALATABILITY

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ABSTRACT

The post-Paleozoic decline of rhynchonelliform brachiopods has been attributed to a variety of factors ranging from competition with bivalves to bioturbation. Of the possible mechanisms invoked to explain the evolutionary decline and cryptic or antitropical distribution of brachiopods, predation has been frequently dismissed due to the potentially low energetic value and suspected non-palatability or toxicity of brachiopod tissues. Here we demonstrate that multiple invertebrate marine predators (crustaceans, echinoderms, and gastropods) are willing and able to consume brachiopods in laboratory settings without any observable negative effects after ingestion. In addition, field samples indicate that predation pressure on the living brachiopod population may be substantial. Although both feeding trials and low energetic values corroborate previous reports that bivalves are preferred prey relative to brachiopods, predation should not be dismissed as a potentially important factor in brachiopod ecology and evolution. The results presented herein reveal that in some cases brachiopods appear to be the intended target of predatory attacks, especially in habitats where mollusks are rare or absent. Examination of the fossil record of predation on rhynchonelliform brachiopods is consistent with this interpretation: evidence for both drilling and repair of brachiopod shells is found throughout the fossil record in multiple orders. While it is likely that predation traces on post-Paleozoic brachiopods are typically rare, there are multiple reports of fossil localities with anomalously high drill hole or repair scar frequencies. This suggests that although brachiopods may be unwanted prey in the presence of energetically more desirable targets, they do appear to be edible and are subject to intense predator-prey interactions under certain conditions.

INTRODUCTION

The post-Paleozoic decline in diversity and abundance of rhynchonelliform brachiopods (Subphylum Rhynchonelliformea, which includes all of the former Class Articulata and some minor groups), in conjunction with the radiation of bivalves, has generated multiple causative hypotheses including: (1) incumbent replacement by (Rudwick 1970; Steele-Petrovic 1979; Gould and Calloway 1980; Sepkoski 1996), or competition with (Thayer 1985), bivalves; (2) increase in depth/intensity of bioturbation (Thayer 1979; Witman and Cooper 1983); and (3) intensification of predation (Stanley 1974, 1977, 1979; Witman and Cooper 1983; Fouke and

LaBarbera 1986; Donovan and Gale 1990). The "predation hypothesis" is particularly controversial (see explanation below).

Here, we combine experimental, neontological, and paleontological data to assess brachiopods as viable prey. Are they non-edible, acceptable, or attractive targets for predators? By answering this question, we can improve our understanding of the role of predation in shaping evolutionary history, ecology, and the present-day biogeography of brachiopods. This is also of interest, as wide spectrum of ecological and evolutionary hypotheses regarding rhynchonelliforms have been advocated in the literature, from those perceiving predation as a primary evolutionary and ecological force, to those dismissing it as negligible.

On one hand, increasing predation pressure during the Mesozoic Marine Revolution (Vermeij 1977) offers a compelling causative model for the failure of brachiopods to recover following the end-Permian and end-Triassic mass extinctions and their subsequent purported shift to refugia from predation (Stanley 1974, 1977, 1979; Witman and Cooper 1983; Donovan and Gale 1990). Evidence supporting this hypothesis consists of: (1) the coincident timing of the appearance and radiation of important groups of predators such as crabs, teleost fishes, asteroids, and gastropods (Stanley 1974; Witman and Cooper 1983; Donovan and Gale 1990, but see Vermeij 1990 for an additional discussion of the timing of asteroid radiations, and Gould and Calloway 1980); (2) the apparent physical vulnerability of brachiopods to predation, being small and thin shelled relative to bivalves (see Stanley 1974, 1977); (3) the current occupation of cryptic habitats by some brachiopods (Stanley 1974, 1977; Witman and Cooper 1983; Donovan and Gale 1990; Zuschin and Mayrhofer 2009; but see Thayer and Allmon 1990; James et al. 1992); (4) the geographic restriction of modern brachiopods, i.e., greater diversity in temperate and polar latitudes (Richardson 1997a; Logan 2007; but see Kowalewski et al. 2002); and (5) the consumption of brachiopods by post-Paleozoic (and especially modern) predators (Witman and Cooper 1983; Fouke and LaBarbera 1986; Harper 2005).

On the other hand, predation has been dismissed by some as a viable explanation for the decline of post-Paleozoic brachiopods because: (1) conclusive evidence that the current restriction of brachiopods to refugia is the result of predation is lacking, and predation on Recent

brachiopods appears to be low; (2) predators exhibit a clear preference for bivalves in laboratory feeding trials, suggesting that processes other than predation (e.g., competition) may have played a more important role in the decline of brachiopods (Thayer 1985); (3) the apparent unwillingness of some modern predators to consume rhynchonelliform brachiopods alludes to chemical defenses (Owen and Williams 1969; McCammon 1972; Thayer 1985; Thayer and Allmon 1990; McClintock et al. 1993; Mahon et al. 2003); and (4) a lack of compelling evidence for predation in the fossil record suggests an early Paleozoic evolution of proposed toxicity (Thayer and Allmon 1990).

Predators' preference for bivalves has been demonstrated by experiments of simultaneous choice (Thayer 1985), or rejection of brachiopod tissue extracts and bioassays (Thayer 1985; Thayer and Allmon 1990; McClintock et al. 1993; Mahon et al. 2003), and have been further interpreted as an indication of brachiopod toxicity. Although both the rejection of brachiopods in favor of bivalves, and the rejection of brachiopod tissues in modern experiments could be due to toxicity, they are also consistent with multiple alternate hypotheses (for example: failure to recognize brachiopods as prey items, the presence of preferred prey, or high inorganic content of the prey). These alternate hypotheses cannot currently be eliminated, as the presence of chemical defenses has not yet been directly substantiated (i.e., isolation of a toxin), and feeding trials using whole, live brachiopods recognizable to *in situ* predators as potential prey are sparse (but see Thayer and Allmon 1990, and Mahon et al. 2003 where some live brachiopods were used).

Based on lack of evidence for predation on both modern and fossil rhynchonellides and terebratulides, a single Paleozoic origin for toxicity prior to the Ordovician divergence of the extant classes of brachiopods has been proposed (Thayer and Allmon 1990), followed by the selective extinction of palatable "articulates" during the Mesozoic due to predation (Thayer 1985; Thayer and Allmon 1990; Mahon et al. 2003). However, both the possibility of a Paleozoic origination of toxicity, and subsequent Mesozoic selection thereof, require re-investigation in light of the developments in brachiopod phylogenetics (e.g., Carlson and Leighton 2001), and the growing body of evidence for predation on rhynchonelliform brachiopods throughout the Phanerozoic (predation traces; for review and data compilations see Alexander 1986a; Leighton 2003b; Kowalewski et al. 2005).

In an effort to improve our understanding of the role of predation in ecology, biogeography, and the evolutionary history of brachiopods, laboratory and meta-analytical approaches were combined to evaluate: (1) the palatability and foraging value of brachiopod prey to durophagous predators, including edibility, energetic value, and prey preference; and (2) the Phanerozoic record of predation based on a comprehensive survey of reported rhynchonelliform predation traces (repair scars and drill holes).

Because the other two subphyla of brachiopods, Linguliformea and Craniiformea, differ in their biogeographical distribution and life mode, they have been excluded from this study.

MATERIALS AND METHODS

The palatability of modern brachiopods was assessed in a series of feeding trials conducted at Friday Harbor Laboratories (Salish Sea, Washington, U.S.A) using common marine invertebrate predators from clades previously documented to attack and consume brachiopods (Mauzey et al. 1968; Witman and Cooper 1983; Fouke and LaBarbera 1986; Richardson 1997b; Harper and Peck 2003; Harper et al. 2009; Harper et al. 2011), exemplifying a variety of predatory strategies from whole ingestion, represented by the sunflower sea star *Pycnopodia helianthoides* (n=4, diameter 28-31 cm) and the hairy triton *Fusitriton oregonensis* (n=8, shell height base of aperture to apex 7-10 cm), to durophagy, represented by the cancrid crab *Cancer productus* (n=3, carapace width 14-20 cm). All organisms were collected via dredging (35-70 m) at Iceberg Point (48°24.741 N; 122°48.600 W), where these predators and prey co-occur *in situ* (with the exception of two individuals of *C. productus*, which were collected in the vicinity of Friday Harbor Laboratories). Seven species of rhynchonelliform brachiopods have been postulated to be unpalatable in previous studies: *Terebratalia transversa, Terebratulina unguicula, Laqueus californianus, Hemithiris psittacea*, found in Puget Sound (Thayer 1985), *Lacazella sp.* and *Thecidellina congregata* from Palau (Thayer and Allmon 1990), and *Liothyrella uva* from the Antarctic (Thayer 1985; McClintock et al. 1993; Mahon et al. 2003). Dredging in Puget Sound yielded two of the aforementioned species: *Terebratalia transversa* (14-34 mm)*,* and *Terebratulina unguicula* (7-18 mm), which were consequently employed in feeding trials. Predators were also offered bivalves supplied in alternation with brachiopods to provide a control

sample for documenting predators' ability to consume known prey under laboratory conditions. As our intent was to evaluate predator's ability and willingness to consume brachiopods, predators were not offered a simultaneous choice between brachiopods and bivalves. Bivalves selected for experiments – *Chlamys hastata* (29-56 mm)*, Clinocardium nuttallii* (13-30 mm)*, and Acila castrensis* (10-16 mm) – are common in Puget Sound (personal observation), live alongside brachiopods (indeed, brachiopods are often found living attached to *C. hastata*), are of similar size to the brachiopods chosen, and would be expected to frequently be consumed by invertebrate marine predators occurring in the region. Organisms were held in open circulation sea tables (1.25 m by 0.5 m) at ~12°C, and given a minimum of five days acclimatization time before experimental trials to ensure that mortality during trials was not the result of trauma. All organisms were carefully examined immediately prior to use in trials to ensure that only live, robust individuals were utilized.

Individual predators were isolated in a sea table and offered sets of monospecific prey in a series of 26 laboratory feeding trials (Table 1) conducted at Friday Harbor Laboratories over two years, with 10 trials run in 2006, and 16 in 2008. Predators were starved for five days prior to feeding to standardize hunger levels. Each experimental feeding is herein referred to as a "trial", which lasted eight days or until all of the prey had been consumed (whichever came first), and was followed by a five day starvation period before the predator was offered a new set of prey from a different species from another clade (i.e., brachiopods or bivalves). As *F. oregonensis* is much smaller and less active than the other two predators, rates of consumption by the gastropods were expected to be notably lower over an eight day trial. Thus, four individual *F. oregonensis* were offered 12 prey individuals in one sea-table per trial; there was no evidence of competition among the gastropods during trials.

In each trial, 12 of the same prey items were arranged into three rows of four similarly sized individuals in a sea-table with a predator. Prey size ranges were consistent across trials within prey species to control for possible size effects. To estimate prey size, the anterior to posterior maximum length of the shell was measured for each individual using digital calipers (± 0.02 mm). The number of prey consumed was recorded each day, however, because *P. helianthoides* and *F. oregonensis* often ingested prey whole, which (in the case of prey ingested

by *P. helianthoides)* sometimes remained alive inside the predator for two to three days, "consumption" was only recorded when prey expelled from the gut of the predator were determined to be dead (i.e., empty shells lacking soft tissue). Predators were observed closely for both immediate and long term adverse effects in response to the ingestion of a toxin if present (as reported for some predators by Thayer 1985). Initially predators were observed for two hours subsequent to the discovery of consumed brachiopod remains, however, as no negative reactions were observed during the first 10 trials (during which all three species of predator consumed brachiopods), subsequent short term monitoring was limited to twice daily. Predators were also monitored for the four weeks following initial brachiopod consumption.

Due to time and space constraints, not all individual predators received the same prey species; each individual predator did, however, take part in a minimum of two trials, where they were offered one species of brachiopod and one species of bivalve (see Table 1). A two-sided Fisher's Exact test was used to determine whether numbers of brachiopods consumed differed statistically from bivalves consumed for each predator species, and overall. A two-sided test was used despite the *a priori* directional prediction of our null hypothesis (i.e., that bivalves are consumed in equal or greater numbers than brachiopods), due to theoretical issues with one-tailed statistical tests (see Lombardi and Hurlbert 2009, Ruxton and Neuhäuser 2010 for a discussion). Significance level was assumed *a priori* at $\alpha=0.05$ and analyses were performed using SAS 9.2 (SAS Institute, Cary, NC).

The organic content of brachiopod tissues relative to bivalves was used as a proxy for the energetic value of prey tissues, and was estimated as the ash-free dry weight (AFDW) of the organism calculated as the ash weight (AW) subtracted from the dry weight (DW). Organic content of internal tissues was estimated using the AFDW for two individuals of the following prey to represent the size range collected for that species (i.e., one large specimen and one small specimen): *C. hastata, C. nuttallii*, and *T. transversa*. Note that because *T. transversa* is punctate, AFDW represents a maximum estimate of potential energetic value, as it includes tissues located in the caeca, which may contain as much as 50% of the total organic tissue content (Curry and Ansell 1986; Curry et al. 1989; Peck and Holmes 1989; James et al. 1992), and is only available to some predators (such as sea stars which ingest prey whole). AFDW was measured as follows;

whole organisms (both shell and tissue) were: (1) placed in a conventional oven at 100°C for 24 hours; (2) weighed (DW); (3) placed in a muffle furnace at 580-600°C for an additional 24 hours; and (4) weighed again (AW). Specimens were cooled in a desiccator before weighing, and were measured using a digital scale to the nearest milligram.

While laboratory feeding trials demonstrate a predator's ability and willingness to consume prey, field surveys can be used to estimate predation pressure on prey communities. Predation traces (repair scars and drill holes) are an effective way to quantitatively assess predator-prey interactions in both living and fossil communities, and are widely used as a proxy for predation intensity (Vermeij 1983; Alexander 1986a; Kowalewski et al. 1998; Leighton 2001b; Kowalewski and Kelley 2002; Leighton 2003b). Therefore, the percentage of individuals with traces (often referred to as either repair or drilling frequency) was used to (1) quantify predation pressure on the local living brachiopod community, and (2) examine the Phanerozoic record of predation on brachiopods.

All live brachiopods and scallops collected from three of the dredges at Iceberg Point were examined in a systematic survey for repair scars to estimate the frequency of durophagous predation on the local brachiopod and bivalve populations (*T. transversa,* n=177; *C. hastata,* n=94; *Chlamys rubida*, n=209). A repair scar is a distortion of ornament growth due to shell breakage resulting from failed lethal predation most likely inflicted by crabs. As repair scars can also result from survival of non-predatory shell breakage, the following criteria were used as to differentiate repairs of predatory origin (Leighton 2001a; Kowalewski 2002): (a) scar shape is non-random (e.g. trapezoidal or circular) reflecting attack structure (e.g., teeth or chelae), (b) the size range of scars is relatively narrow, (c) scar is not concentric with growth lines, or (d) matching scars on both valves (suggests that predator enclosed and attempted to crush prey). Repair frequency was calculated as the number of repaired individuals divided by the sample size. A high repair frequency may be indicative of high predation pressure (Vermeij 1987; see Leighton 2002 for a discussion).

In addition to the modern trace analysis, the Phanerozoic record of both types of predation traces (drill holes and repair scars) was examined by assembling a dataset of species level drilling

and repair frequencies reported in previous studies (based on a comprehensive survey of the literature in December 2010). Literature sources were assembled using major online reference databases (GEOREF, ISI Web of Science, etc.) and books, including both modern and fossil occurrences. The following criteria were used when selecting sources: (1) predation trace frequencies were reported for individual brachiopod species and not pooled by higher taxonomic group (e.g., genus), (2) reports included raw numerical data for a minimum of one species, (3) trace data included drill holes and/or repair scars, (4) sample size per species was at least 10 specimens, and (5) traces were interpreted by original authors as predatory in origin. Both drilling and repair frequencies were calculated per species as the number of individuals with traces divided by the total number of individuals in the sample. If necessary, a correction was made for disarticulated valves by dividing the total sample size by two (see Kowalewski 2002). The use of the above criteria eliminates qualitative (e.g., presence/absence) and small samples from our dataset, and is thus a conservative compilation. Note that drilling and repair frequencies from a sample or locality were not pooled, and that a single publication may contain up to 12 brachiopod species for which repair and/or drilling frequencies are reported. A single publication may also identify only one type of trace (i.e., either drill holes or repair scars), or could report observations of both drilling and repair.

RESULTS

Laboratory Feeding Trials

Brachiopods were consumed by all three species of predators (Tables 1 and 2): *P. helianthoides* consumed 18, *C. productus* 27, and *F. oregonensis* consumed four. Sea stars typically forage by traveling around the sea-table with arms extended until the arms come into contact with prey. As the adult *Pycnopodia* were large enough to encounter multiple prey simultaneously in the sea tables, sea stars were frequently observed handing several prey at once. Once a single individual in a row of prey was detected and attacked by a sea star, nearby prey were promptly detected, and often simultaneously captured and consumed. While feeding on one individual, a sea star may grasp other prey and move them down the ambulacral groove using the tubefeet, toward the mouth. Prey were ingested whole, and when successfully consumed, empty shells were expelled from the gut. Crabs were no less active, and once prey were encountered the crab would move to position itself above the prey to form a cage within the walking legs. This

scrambling behavior frequently resulted in the detection of other nearby prey; if this occurred, the crab would maneuver the additional prey under its carapace. The accumulation of prey would then be sorted through, and one select for consumption, which the crab would attempt to crush between the molars of the chela to gain access to the flesh. Once accessed, the prey was held in front of the mouth by one or both claws for consumption, during which the prey skeleton was typically crushed further into smaller unidentifiable fragments. The predatory behavior of *Fusitriton* differed from the larger, more active sea stars and crabs, in that the gastropods were far less active in foraging. Gastropods traversed gradually along convoluted pathways around the sea table, and did not encounter multiple prey simultaneously. In predatory encounters, gastropods would ingest prey whole, expelling the empty shells.

At least one individual from each species of predator consumed a minimum of two brachiopods; none of the predators exhibited any visible adverse effects as a result of consuming brachiopods after either short-term or long term monitoring (i.e., predators continued to behave and eat normally). Both *C. productus* and P. *helianthoides* consumed a significantly greater quantity of bivalves than brachiopods ($p \ll 0.0001$), while *Fusitriton* did not ($p = 0.20$). Also, when data from all trials and predator types were pooled, bivalves were consumed in significantly greater numbers than brachiopods overall ($p \ll 0.0001$). Out of the 132 brachiopods offered to predators, 49 were consumed (37%), whereas 160 out of the 192 bivalves offered to predators (83%) were consumed.

Organic Content Estimates

The organic content measured using the AFDW of the brachiopod *T. transversa* ranged from 3-5% (Table 3). Organic content of the bivalve *C. hastata* was 5% for both the small and large specimen, and 4-10% for the bivalve *C. nuttallii*.

Modern Repair Frequency

Out of 177 live brachiopods (*T. transversa*) examined in the systematic surveys of dredge material, repair scars categorized as predatory in origin were observed on 50 individuals (29%). Out of the 94 live *C. hastata* examined, repair scars were observed on four individuals (4%), and out of the 209 live *C. rubida* examined, repair scars were observed on four individuals (2%).

Repair frequencies did not vary notably across dredge samples for brachiopods (36%, 21%, and 24%) or bivalves (2%, 2%, and 3%).

Phanerozoic Predation Traces

The Phanerozoic database of predation trace frequencies for rhynchonelliform brachiopods was assembled from 27 sources (Appendix A), and included reports of predation in the late Cambrian to the Recent from 37 localities (Figure 2). The database yielded 131 reported trace frequencies (Appendix B), 67 of which were reports of drill holes, and 73 of which were reports of repair scars. Traces were reported for 94 species, representing 71 genera and eight orders (Table 4). The majority of trace frequencies were reported for Paleozoic samples (n=108), including trace frequencies as high as 64% (a report of drilling in the Devonian by Smith et al. 1985; see Figure 2). Due to a dearth of sources reporting Mesozoic traces, the database only contains two Mesozoic drilling frequencies (2.8% and 2.3%, both Jurassic; Kowalewski et al. 1998). There were 21 Cenozoic trace frequencies reported, 17 of which were drill holes and 7 were repair scars (the highest of which was a report of a 48% drilling frequency at a Miocene locality; Baumiller and Bitner 2004).

DISCUSSION

In laboratory feeding trials, not only were brachiopods consumed by all three species of predator, but they were consumed in greater quantities than anticipated (based on reports in the literature). To our knowledge the observations reported herein represent the second documented case of directly observed decapod predation on rhynchonelliform brachiopods (see Fouke and LaBarbera 1986, who observed consumption by crustaceans). Previous reports of durophagous predation on brachiopods have been inferred predominantly from repair scars (e.g., Brunton 1966; Alexander 1981; Alexander 1986a; Alexander 1986b; Alexander et al. 1992; Harper 2005; Harper et al. 2009).

Results are congruent with previous assessments that brachiopods are not preferred prey (Thayer 1985; Peck 1993); bivalves were consumed in significantly greater numbers over similar intervals of time by all three species of predators ($p \ll 0.0001$). However, the observed number of brachiopods consumed in this study was far greater than previously observed for the same species

by Thayer (1985), who reported that *P. helianthoides* consumed five, *C. productus* consumed one, and *F. oregonensis* consumed zero brachiopods, respectively. The much greater number of brachiopods consumed reported here may, in part, be due to predator recognition of brachiopods as viable prey: (1) unlike previous studies (Thayer 1985; Thayer and Allmon 1990; Mahon et al. 2003), *all* brachiopods offered to predators in experimental trials were live; (2) predators used in experimental trials were collected from habitats in which brachiopods were present; and (3) the sequential nature of the feeding trials could have facilitated a willingness to consume brachiopods (as our study was primarily aimed at testing brachiopod palatability and predators' *ability* to consume brachiopods, predators were never offered a simultaneous choice between brachiopods and bivalves).

While the consumption of brachiopods by predators is sometimes attributed to either accidental ingestion due to proximity with intended prey or inexperience (e.g., Kowalewski et al. 2005; Simoes et al. 2007), neither is likely to explain the attacks observed in the laboratory experiments, as predators were only offered monospecific groups of prey. In addition, the predators were all adults collected from habitats where brachiopods are abundant, and thus, unlikely to ingest them due to inexperience with the prey.

These successful feeding trials demonstrate that a variety of common marine invertebrate predators are willing to consume *T. transversa* and *T. unguicula,* two species of temperate rhynchonelliform brachiopods repeatedly, in surprisingly large numbers, and without any observable detrimental effects after ingestion. These data do not support the hypothesis that rhynchonelliform brachiopods have evolved chemical defenses (Owen and Williams 1969) and are inconsistent with previous reports that *T. transversa* and *T. unguicula* are repellant (Thayer 1985). Alternatively, it is possible that these particular invertebrate predators have evolved a tolerance for the toxin if present (e.g., the Colorado potato beetles evolved resistance to pesticides), or are capable of handling it in small doses; however, this seems unlikely in light of the long history of the co-occurrence of abundant alternative prey (e.g., bivalves).

As discussed earlier, chemical defenses are not the only explanation for the rejection of brachiopod tissue. Optimal foraging predicts that predators should maximize their net energy

gain (calculated as the difference between the energetic benefit and the cost, divided by handling time). That is, the energy required to locate, attack, and consume a prey item (cost) is low relative to the caloric value (benefit) with respect to handling time (Krebs 1977; Stephens and Krebs 1986; Leighton 2002). Although biological systems may frequently be too complex for optimal foraging to apply, the amount of energy gained is nonetheless an important factor in prey selection. Brachiopods may be of less benefit to predators relative to bivalves due simply to low tissue density and low organic content of some brachiopods (Thayer 1985; Peck 1993), and not due to chemical defenses. Some brachiopod species have greater inorganic content due to the spiculation of brachiopod tissues (James et al. 1992; Peck 1993), although spicules have not been observed in *T. transversa*, while in other species tissue located in the caeca is unavailable to many predators (such as crabs). Indeed, the organic content of *T. transversa* estimated in this study was lower than that of the similarly-sized bivalve *C. nuttallii*, and within the range observed by Peck (1993).

While the organic content data reported here represent an approximation for the targeted taxa, and are by no means a test of the aforementioned hypothesis, they do corroborate the results of Peck (1993), and suggest worthwhile avenues for additional investigation, as low organic content (equating to lower benefit to the predator) provides an alternative explanation to chemical defenses for prey preference and low predation pressure.

The repair frequency observed in the systematically sampled living brachiopod population was congruent with the feeding trial data, and illustrates predator familiarity with brachiopods as prey in their natural habitat. Predators were most likely crabs, as matching scars were often found on both valves suggesting that they were made by a scissor-like weapon, such as crab chelae (Kowalewski 2002). Although 29% might be considered an anomalously high repair frequency for brachiopods, there have been similar reports for durophagy on extant rhynchonelliform brachiopods (e.g., Harper et al. 2009). The low repair frequency observed in the living scallop population may either reflect the fact that some scallops are able to actively flee predatory attacks via swimming, or low survival rates (they may be so vulnerable to durophagous predation that once captured, the majority are killed). These data are not intended to compare predation

intensity between brachiopods and bivalves; repair frequencies are used simply to document that predatory attacks do occur in the brachiopod population with some frequency.

It is important to note that repair frequency constitutes a conservative estimate of predation pressure, as: (1) survival of bivalved animals after a failed attack is unlikely due to diminished repair capability and once damaged, individuals leak body fluids (attracting other predators) or perish (Vermeij 1983; Alexander et al. 1992); (2) repairs only record durophagous predation excluding other types of predatory attacks that do not leave traces such as whole ingestion; (3) repair frequency only estimates number of failed attacks, and actual attack frequency may be much greater if successful attacks outnumber failed attacks (in instances where predators have evolved increased effectiveness). Although the interpretation of repair frequency remains ambiguous – high frequencies could indicate either intense predation (organism is common prey, or predators are abundant) or evolved prey defenses and prey regularly surviving attacks (Vermeij 1987; Kowalewski 2002; Leighton 2002) – repairs nevertheless do record predator attacks, and in this case demonstrate that predatory attacks on brachiopods occur with notable frequency in modern benthic communities. Furthermore, a variety of predators attack and consume brachiopods including echinoids and fish (Witman and Cooper 1983; Fouke and LaBarbera 1986), asteroids (Mauzey et al. 1968; Richardson 1997b), ophiuroids (Fouke and LaBarbera 1986), crustaceans (Fouke and LaBarbera 1986; Harper et al. 2009), and gastropods (Witman and Cooper 1983; Harper and Peck 2003; Harper et al. 2011). This, in conjunction with the feeding trial and repair scar data, suggests that predation pressure on modern temperate brachiopods may be substantial under certain conditions.

Although some data suggest that in most cases predatory pressure on brachiopods is negligible (Delance and Emig 2004; Kowalewski et al. 2005; Simoes et al. 2007), the importance of predation in brachiopod ecology, biogeography, and evolution cannot be dismissed outright, given that predation can be very important locally. Predation trace data document that brachiopods are indeed attacked and consumed by predators, in some localized cases in very high quantities (Smith et al. 1985; Baumiller and Bitner 2004; Delance and Emig 2004; Baumiller et al. 2006; Harper et al. 2009; Schimmel et al. *In Press*). In addition, many traits of modern brachiopod species are consistent with the hypothesis that they represent evolved defense against

predation, these include: (1) low flesh yield (Thayer 1985; Peck 1993); (2) inaccessible tissue (located in caeca; Curry and Ansell 1986); (3) high inorganic tissue content (spicules in some species; Peck 1993); and (4) tight articulation and the lack of a permanent gape. Additional traits may represent evolved defenses, and have been observed in numerous fossil brachiopod species. These include: (1) shell ornament, such as ribs and spines, to deter durophagy (Signor and Brett 1984; Leighton 1999); (2) robust peduncular musculature facilitating a stronger attachment to the substrate, and preventing shell access though the pedicle opening (Bambach 1999); and (3) the secretion of deltidial plates around the pedicle opening, also preventing access to the shell through the pedicle (Bambach 1999). As it has been suggested that asteroid predation could have played an important role in the decline of post-Paleozoic rhynchonelliforms (Donovan and Gale 1990), it is worth noting that tight articulation proved particularly important in the laboratory feeding trials described herein, allowing several brachiopods to survive ingestion by sea stars. During the mid-Paleozoic, a time of a postulated increase in predation (Signor and Brett 1984), brachiopod groups possessing ornament and other potential defenses (Leighton 2001b, 2003a) became increasingly more diverse and common (Alexander 1977; Signor and Brett 1984; Alexander 1986b; Leighton 2003b) and continued diversifying thereafter. Similarly, consistent with predictions for the effects of predation on geographic distribution (greater predation in the Tropics), the proportion of spinose brachiopod genera increases with decreasing latitude during the Devonian (Leighton 1999) and the Mississippian (Dietl and Kelley 2001).

Examination of the Phanerozoic history of brachiopod predation traces reveals an extensive record of both types of traces on rhynchonelliform brachiopods. While interpretation of temporal trends is beyond the scope of this study, they do serve to illustrate the considerable breadth of predation on brachiopods. Quantitative data on predation traces exist for all but two Phanerozoic periods (the Triassic and Cretaceous), the occurrence of traces is geographically widespread, and traces have been observed in multiple rhynchonelliform orders. In addition, there have been multiple reports of predation traces occurring in two of the three extant orders (Rhynchonellida and Terebratulida). If toxicity evolved before the Ordovician divergence of extant clades (Thayer and Allmon 1990), this would imply toxicity in Rhynchonellida, Atrypida, Spiriferida/Spiriferinida, Thecideida, Athyridida, and Terebratulida (based on the phylogeny of Carlson and Leighton 2001) all of which, with the exception of Thecideides, have a robust record

of predation traces (Table 4). Assuming that even some of these groups are not toxic, the evolution of toxicity prior to the Ordovician would require that the trait to be lost multiple times independently. If Thecideides are indeed toxic, as proposed by Thayer and Allmon (1990), a more parsimonious explanation would be that toxicity evolved independently in Thecideides sometime in the Mesozoic.

In the database of reported predation traces from the literature, we observed that studies were overwhelmingly focused on Paleozoic brachiopods (see Figure 2), and there is a pronounced lack of reported trace data during the Mesozoic, making it difficult to examine the role of predation in Mesozoic brachiopod evolution and diversity. This dearth of trace data could reflect a genuine signal, i.e., an absence of predation traces indicating either increased predator success or a decrease in attack frequency in the case of durophagy, or low predation in the case of drilling. It is worth noting that the dearth of reports of Mesozoic predation traces overlaps with the Mesozoic Marine Revolution, a time of proposed increased predation pressure (Vermeij 1977), and that there are several reported values of predation trace frequencies in Cenozoic assemblages similar to those typically seen in the Paleozoic. In addition, quantitative data on predation traces are generally lacking for marine invertebrate prey during the Triassic and Jurassic (see Huntley and Kowalewski 2007). However, the lack of both kinds of trace data (drill holes and repair scars) is more likely to be the result of insufficient reports in the literature. Additional studies of Mesozoic predation targeting brachiopods are needed to evaluate the role of predation more fully during this time interval.

Although traces are numerous, the majority of studies we examined reported trace frequencies below 10% (see Figure 2). However, compilations of reported data such as this one are difficult to interpret. Studies of predation are likely to target localities with known traces, and sampling strategies are often designed to target species or genera with known traces as opposed to a systematic sampling more appropriate for large scale spatio- temporal comparisons (Kowalewski et al. 2005). In addition, trace frequencies that are so low as to be determined insignificant or negligible may be omitted from the final published report. Alternatively, it has been suggested that as studies of brachiopod predation in general are lacking, all occurrences of traces are likely to be reported (Harper et al. 2011). If, however, predation trace frequency on

brachiopods is typically low (as suggested by Kowalewski et al. 2005), then the question becomes, what factors cause brief periods of anomalously high localized predation? Localities with high predation rates could represent prey-rank abundance patterns. For example, predator preference for other prey (such as bivalves) would result in low trace frequencies in mixed assemblages where preferred prey types are abundant, and high trace frequencies in assemblages dominated by brachiopods. Indeed, Hoffmeister et al. (2004) noted that mollusk bivalves were drilled at higher frequencies than sympatric brachiopods in fossil samples collected from the Permian of West Texas. A similar pattern has also been observed in present-day brachiopod-bivalve death assemblages of the outer Brazilian Shelf (Simoes et al. 2007). Additional studies targeting mixed brachiopod bivalve assemblages with variable abundances of preferred prey types are needed to assess this hypothesis.

Although we did not find behavioral evidence supporting the presence of chemical defenses, brachiopods do not appear to be preferred prey and repellency aside, may in fact be well-defended prey through passive defenses. If the current biogeographic distribution of brachiopods is not the result of predation, it may be a consequence of environmental tolerances (Thayer and Allmon 1990), or simply the geographic region from which these groups originated and diversified (Richardson 1997a).

CONCLUSIONS

(1) In feeding experiments whole, live brachiopods were willingly consumed by three common marine invertebrate predators (crustaceans, echinoderms, and gastropods) with no visible adverse effects, contrary to the widely held belief that modern brachiopods are toxic.

(2) Systematic field surveys examining the frequency of predation traces (repair scars) on the local brachiopod population, signify that predation pressure in the brachiopod community may be noteworthy.

(3) The fossil record yields a plethora of quantitative data documenting an extensive history of predation on brachiopods.

(4) Predation should still, therefore, be considered a potentially important factor in brachiopod ecology and evolution.

FIGURES AND FIGURE CAPTIONS

Figure 1. Trace frequencies reported in the literature within brachiopod orders. Each dot represents a single trace frequency report: (A) repair frequencies within each brachiopod order; (B) drilling frequencies; (C) proportions of trace types, light gray denotes proportion of all traces that are drill holes, and dark gray denotes the proportion of all traces that are repair scars.
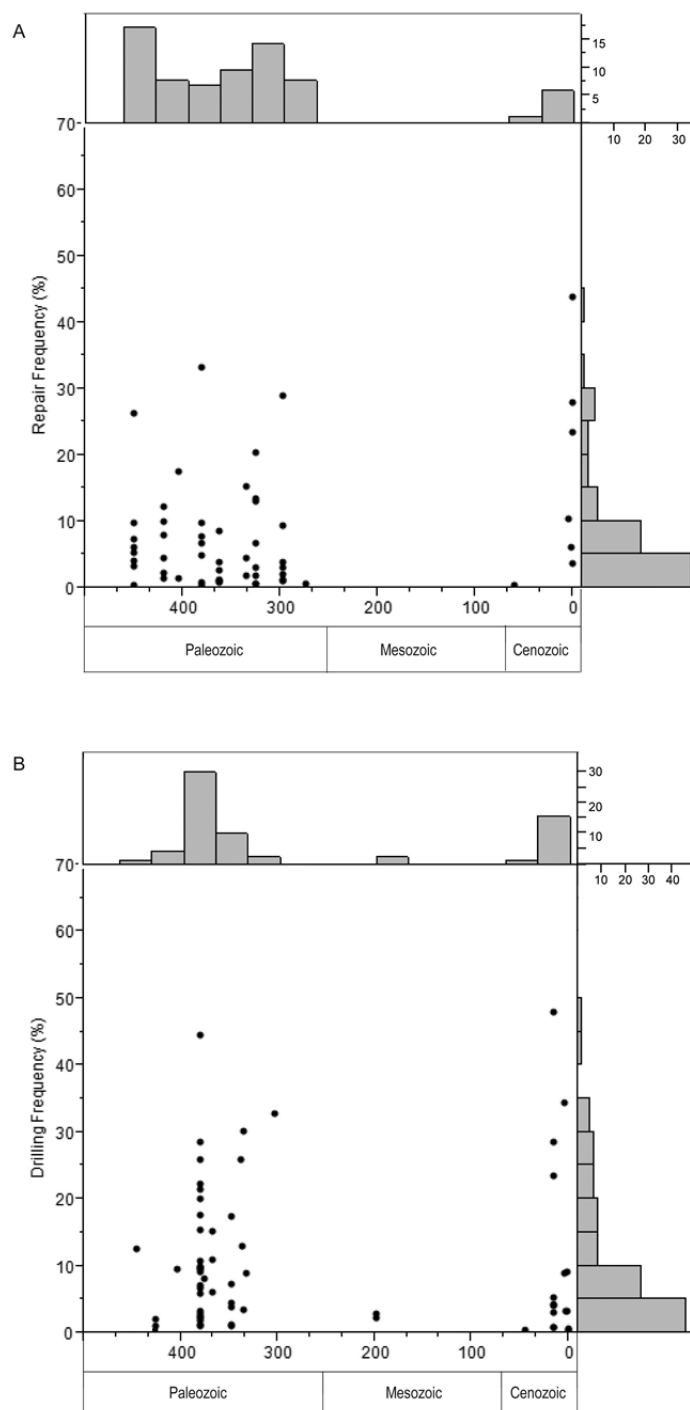
Figure 2. Distribution and abundance of (A) repair frequencies, and (B) drilling frequencies through geologic time. Frequency histograms are shown for both axes. Reports of predation on Mesozoic brachiopods are clearly lacking, and the vast majority of reports are of predation on Paleozoic brachiopods. Note that the majority of species level trace frequencies reported in the literature are less than 10%.

TABLES AND TABLE CAPTIONS

Table 1. Individual feeding trial results. An individual predator was offered brachiopods in alternation with bivalves, thus each series of trials (numbered 1 through 4) involves a single unique predator, with the exception of *F. oregonensis* where two groups of four gastropods were used in each set of trials.

Predator	Trial	Prey	Prey Clade	Offered	Consumed
P. helianthoides	1	*C. hastata*	Bivalvia	12	12
	2	*T. transversa*	Brachiopoda	12	2
	3	*A. castrensis*	Bivalvia	12	10
P. helianthoides	1	*C. hastata*	Bivalvia	12	12
	2	*T. transversa*	Brachiopoda	12	0
	3	*A. castrensis*	Bivalvia	12	12
P. helianthoides	1	*T. transversa*	Brachiopoda	12	3
	2	*C. hastata*	Bivalvia	12	12
	3	*T. transversa*	Brachiopoda	12	5
	4	*C. nuttalllii*	Bivalvia	12	12
P. helianthoides	1	*C. hastata*	Bivalvia	12	12
	2	*T. transversa*	Brachiopoda	12	8
	3	*C. nuttalllii*	Bivalvia	12	12
C. productus	1	*A. castrensis*	Bivalvia	12	8
	2	*T. transversa*	Brachiopoda	12	3
C. productus	1	*C. nuttalllii*	Bivalvia	12	10
	2	*T. transversa*	Brachiopoda	12	3
	3	*C. hastata*	Bivalvia	12	12
C. productus	1	*C. hastata*	Bivalvia	12	12
	2	*T. transversa*	Brachiopoda	12	9
	3	*C. nuttalllii*	Bivalvia	12	12
	4	*T. transversa*	Brachiopoda	12	12
F. oregonensis	1	*A. castrensis*	Bivalvia	12	2
(n=4)	2	*T. unguicula*	Brachiopoda	12	4
F. oregonensis	1	*T. transversa*	Brachiopoda	12	0
(n=4)	2	*C. nuttalllii*	Bivalvia	12	0

Table 2. Summary showing total numbers and percentages of prey consumed by predator species. There was a significant difference between the number of brachiopods and bivalves consumed by crabs and sea stars as determined by a Fisher's Exact test (p<<0.0001), but not for gastropods (p=0.21). The total number of bivalves consumed by all predators in all trials is also significantly greater (*p<<0.0001*).

Predator	Prey Type	Genus	Offered	Consumed	% Consumed
P. helianthoides	Bivalvia	*C. hastata*	48	48	100%
		A. castrensis	24	22	92%
p<<0.0001		*C. nuttalllii*	24	24	100%
	Brachiopoda	*T. transversa*	60	18	30%
		T. unguicula	0	.	.
C. productus	Bivalvia	*C. hastata*	24	24	100%
		A. castrensis	12	8	67%
p<<0.0001		*C. nuttalllii*	24	22	92%
	Brachiopoda	*T. transversa*	48	27	56%
		T. unguicula	0	.	.
F. oregonensis	Bivalvia	*C. hastata*	0	.	.
		A. castrensis	12	2	17%
p=0.21		*C. nuttalllii*	12	0	0%
	Brachiopoda	*T. transversa*	12	0	0%
		T. unguicula	12	4	33%
Total	**Bivalvia**		**192**	**160**	**83%**
p<<0.0001	**Brachiopoda**		**132**	**49**	**37%**
		Total	**324**	**199**	

Table 3. Amount of organic material present by taxon. AFDW was measured for one large and one small individual, representative of the size range of specimens used in feeding trials.

Species	AFDW (g)	% Organic
C. hastata (large)	1.4101	5.3%
C. hastata (small)	0.5231	5.3%
T. transversa (large)	0.2423	3.5%
T. transversa (small)	0.0890	5.2%
C. nuttallii (large)	0.0968	4.4%
C. nuttallii (small)	0.1320	10.6%

Table 4. Summary of compiled predation trace frequencies from the literature by order. Asterisk denotes extant orders of brachiopods; N (sp) is the number of species within that order with reported predation traces; n is total number of all individuals within that order examined for traces (i.e., pooled sample size); Mean is the mean trace frequency (sum of species level trace frequencies divided by the number of trace frequencies reported); SD is standard deviation; Min is the lowest species level trace frequency reported within that order; Max is the highest species level trace frequency reported within that order. Note that both types of predation traces have been documented in 8 of the 18 rhynchonelliform orders.

	Order	N (sp)	n	Mean	SD	Min	Max
Drilling Frequencies	Athyridida	16	3,366	8%	6	1%	21%
	Atrypida	4	838	4%	3	1%	6%
	Orthida	9	7,337	10%	8	1%	26%
	Productida	3	344	10%	14	1%	26%
	Rhynchonellida*	2	125	8%	7	3%	13%
	Spiriferida	7	704	9%	6	1%	18%
	Strophomenida	7	1,273	23%	13	8%	44%
	Terebratulida*	18	18,369	12%	15	0.3%	48%
Repair Scar Frequencies	Athyridida	6	1,844	4%	5	1%	13%
	Atrypida	4	723	5%	3	2%	8%
	Orthida	11	3,662	4%	2	0.44%	6%
	Productida	5	951	11%	11	1%	29%
	Rhynchonellida*	3	842	2%	3	0.4%	5%
	Spiriferida	7	1,419	2%	2	0.48%	5%
	Strophomenida	22	5,721	11%	9	1%	33%
	Terebratulida*	7	5,697	17%	16	1%	44%

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APPENDIX A

SOURCE LITERATURE FOR DATABASE COMPILATION AND TYPES OF PREDATION TRACES REPORTED

Source	Repair Scars	Drill Holes
Alexander, R. R. 1981. Predation scars preserved in Chesterian brachiopods: probable culprits and evolutionary consequences for the articulates. Journal of Paleontology 55(1):192-203.	x	
Alexander R. R. 1986. In *Les Brachiopodes fossiles et actuels*, (eds.) Racheboeuf P. R., Emig C. C. (Université de Bretagne Occidentale, Brest, France), pp 159-167.	x	
Alexander, R. R. 1986. Resistance to and repair of shell breakage induced by durophages in Late Ordovician brachiopods. Journal of Paleontology 60(2):273-285.	x	
Ausich, W. I., and R. A. Gurrola. 1979. 2 Boring organisms in a Lower Mississippian community of southern Indiana. Journal of Paleontology 53(2):335-344.		x
Baumiller, T. K., and M. A. Bitner. 2004. A case of intense predatory drilling of brachiopods from the Middle Miocene of southeastern Poland. Palaeogeography, Palaeoclimatology, Palaeoecology 214(1-2):85-95.		x
Baumiller, T. K., M. A. Bitner, and C. C. Emig. 2006. High frequency of drill holes in brachiopods from the Pliocene of Algeria and its ecological implications. Lethaia 39(4):313-320.		x
Bitner, M. A. 2000. Lower Eocene (Middle Ilerdian) brachiopods from the Campo region, Central Pyrenees, north-eastern Spain. Revista Espanola de Paleontologia 15:117-128.		x
Brunton, H. 1966. Predation and shell damage in a Visean brachiopod fauna. Palaeontology 9(3):355-359.		x
Brunton, C. H. C., and C. Champion. 1974. A lower Carboniferous brachiopod fauna from the Manifold Valley, Staffordshire. Palaeontology 17:811-840.		x
Buehler, E. J. 1969. Cylindrical borings in Devonian shells. Journal of Paleontology 43(5):1291.		x
Delance, J. H., and C. C. Emig. 2004. Drilling predation on *Gryphus vitreus* (Brachiopoda) off the French Mediterranean coasts. Palaeogeography, Palaeoclimatology, Palaeoecology 208(1-2):23-30.		x
Deline, B., T. Baumiller, P. Kaplan, M. Kowalewski, and A. P. Hoffmeister. 2003. Edge-drilling on the brachiopod Perditocardinia cf. P-dubia from the Mississippian of Missouri (USA). Palaeogeography, Palaeoclimatology, Palaeoecology 201(3-4):211-219.		x
Donovan, S. K., and D. A. T. Harper. 2007. Rare borings in Pleistocene brachiopods from Jamaica and Barbados. Caribbean Journal of Science 43(1):59-64.		x
Harper, E. M. 2005. Evidence of predation damage in Pliocene *Apletosia maxima* (Brachiopoda). Palaeontology 48:197-208.	x	x
Harper, E. M., L. S. Peck, and K. R. Hendry. 2009. Patterns of shell repair in articulate brachiopods indicate size constitutes a refuge from predation. Marine Biology 156(10):1993-2000.	x	

Hoffmeister, A. P., M. Kowalewski, R. K. Bambach, and T. K. Baumiller. 2003. Intense drilling in the Carboniferous brachiopod *Cardiarina cordata* Cooper, 1956. Lethaia 36(2):107-117.		x
Kaplan, P., and T. K. Baumiller. 2000. Taphonomic inferences on boring habit in the richmondian *Onniella meeki* epibole. Palaios 15(6):499-510.		x
Kowalewski, M., A. Dulai, and F. T. Fursich. 1998. A fossil record full of holes: The Phanerozoic history of drilling predation. Geology 26(12):1091-1094.	x	
Leighton, L. R. 2001. New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success. Palaeogeography Palaeoclimatology Palaeoecology 165(1-2):53-69.		x
Leighton, L. R. 2003. Morphological response of prey to drilling predation in the Middle Devonian. Palaeogeography, Palaeoclimatology, Palaeoecology 201(3-4):221-234.		x
Mottequin, B., and G. Sevastopulo. 2009. Predatory boreholes in Tournaisian (Lower Carboniferous) spiriferid brachiopods. Lethaia 42(3):274-282.		x
Rohr, D. M. 1976. Silurian predator borings in brachiopod Dicelosia from Canadian Arctic. Journal of Paleontology 50(6):1175-1179.		x
Ruggiero, E. T. 1999. Bioerosive processes affecting a population of brachiopods (Upper Pliocene, Apulia). Bulletin of Geological Society of Denmark 45(2):169-172.		x
Ruggiero, E. T., and P. Raia. 2010. Bioerosion structures and their distribution on shells of the Lower Pleistocene terebratulid brachiopod *Gryphus minor*. Palaeogeography, Palaeoclimatology, Palaeoecology 293(1-2):157-166.	x	
Schimmel, M., Kowalewski, M., and Coffey, B. *In Press*. Traces of predation/parasitism recorded in Eocene brachiopods from the Castle Hayne Limestone, North Carolina, USA. Lethaia in press.		x
Sheehan, P. M., and P. J. Lesperance. 1978. Effect of predation on population-dynamics of a Devonian brachiopod. Journal of Paleontology 52(4):812-817.		x
Simoes, M. G., C. S. Rodrigues, and M. Kowalewski. 2007. Comparative analysis of drilling frequencies in recent brachiopod-mollusk associations from the southern Brazilian shelf. Palaios 22:143-154.		x
Smith, S. A., C. W. Thayer, and C. E. Brett. 1985. Predation in the Paleozoic: Gastropod-like drillholes in Devonian brachiopods. Science 230(4729):1033-1035.		x

APPENDIX B

PREDATION TRACE FREQUENCIES

Citation	Species	Trace Type	Trace Freq. (%)	Age (MA)	Geologic Period
Ausich and Gurrola, 1979	*Athyris lamellosa*	Drillhole	4	348	Mississippian
Buehler, 1969	*Athyris spiriferoides*	Drillhole	2	381	Devonian
Smith et al., 1985	*Athyris spiriferoides*	Drillhole	21	381	Devonian
Smith et al., 1985	*Athyris spiriferoides*	Drillhole	15	381	Devonian
Smith et al., 1985	*Athyris spiriferoides*	Drillhole	6	381	Devonian
Smith et al., 1985	*Athyris spiriferoides*	Drillhole	15	381	Devonian
Smith et al., 1985	*Athyris spiriferoides*	Drillhole	2	381	Devonian
Smith et al., 1985	*Athyris spiriferoides*	Drillhole	7	381	Devonian
Ausich and Gurrola, 1979	*Cleiothyridina parvirostra*	Drillhole	4	348	Mississippian
Ausich and Gurrola, 1979	*Composita globosa*	Drillhole	7	348	Mississippian
Smith et al., 1985	*Meristella haskinsi*	Drillhole	9	381	Devonian
Smith et al., 1985	*Meristella haskinsi*	Drillhole	3	381	Devonian
Smith et al., 1985	*Nucleospira concinna*	Drillhole	7	381	Devonian
Smith et al., 1985	*Nucleospira concinna*	Drillhole	3	381	Devonian
Ausich and Gurrola, 1979	*Torynifer pseudolineata*	Drillhole	17	348	Mississippian
Ausich and Gurrola, 1979	*Tylothyris sp.*	Drillhole	1	348	Mississippian
Leighton, 2001	*Pseudoatrypa devoniana*	Drillhole	6	367	Devonian
Smith et al., 1985	*Pseudoatrypa devoniana*	Drillhole	2	381	Devonian
Smith et al., 1985	*Pseudoatrypa devoniana*	Drillhole	6	381	Devonian
Smith et al., 1985	*Pseudoatrypa devoniana*	Drillhole	1	381	Devonian
Rohr, 1976	*Dicaelosia sp.*	Drillhole	1	426	Silurian
Rohr, 1976	*Dicaelosia sp.*	Drillhole	2	426	Silurian
Sheehan and Lesperance, 1978	*Discomyorthis musculosa*	Drillhole	10	404	Devonian
Rohr, 1976	*Epitomyonia*	Drillhole	1	426	Silurian
Kaplan, 2000	*Onniella meeki*	Drillhole	12	445	Ordovician
Smith et al., 1985	*Rhipidomella sp.*	Drillhole	20	381	Devonian
Smith et al., 1985	*Rhipidomella sp.*	Drillhole	26	381	Devonian
Smith et al., 1985	*Rhipidomella sp.*	Drillhole	11	381	Devonian
Smith et al., 1985	*Rhipidomella sp.*	Drillhole	10	381	Devonian
Deline et al, 2003	*Perditocardinia dubia*	Drillhole	26	339	Mississippian
Brunton, 1966	*Rugosochonetes celticus*	Drillhole	4	335	Mississippian
Ausich and Gurrola, 1979	*Rugosochonetes planumbona*	Drillhole	1	348	Mississippian
Kowalewski et al, 1998	*Calcirhynchia plicatissima*	Drillhole	3	199	Jurassic
Brunton, 1974	*Lambdarina manifoldensis*	Drillhole	13	337	Mississippian
Mottequin, 2009	*Crurithyris sp.*	Drillhole	9	332	Mississippian

Smith et al., 1985	*Cyrtina hamiltonensis*	Drillhole	10	381	Devonian
Smith et al., 1985	*Cyrtina hamiltonensis*	Drillhole	1	381	Devonian
Smith et al., 1985	*Mediospirifer audaculus*	Drillhole	18	381	Devonian
Smith et al., 1985	*Mediospirifer audaculus*	Drillhole	2	381	Devonian
Smith et al., 1985	*Parazyga hirsuta*	Drillhole	10	381	Devonian
Smith et al., 1985	*Spinatrypa spinosa*	Drillhole	10	381	Devonian
Leighton, 2001	*Devonoproductus walcotti*	Drillhole	11	367	Devonian
Leighton, 2001	*Douvillina arcuata*	Drillhole	15	367	Devonian
Smith et al, 1985	*Douvillina inequistriata*	Drillhole	29	381	Devonian
Leighton, 2003	*Pholidostrophia*	Drillhole	8	375	Devonian
Smith et al., 1985	*Pholidostrophia nacrea*	Drillhole	22	381	Devonian
Smith et al., 1985	*Pholidostrophia nacrea*	Drillhole	44	381	Devonian
Brunton, 1966	*Productina margaritacea*	Drillhole	30	335	Mississippian
Harper, 2005	*Apletosia maxima*	Drillhole	9	4	Tertiary
Donovan, 2007	*Argyrotheca barrettiana*	Drillhole	9	2	Tertiary
Baumiller and Bitner, 2004	*Argyrotheca cordata*	Drillhole	4	15	Tertiary
Baumiller and Bitner, 2004	*Argyrotheca cordata*	Drillhole	1	15	Tertiary
Baumiller and Bitner, 2004	*Argyrotheca cuneata*	Drillhole	3	15	Tertiary
Baumiller and Bitner, 2004	*Argyrotheca cuneata*	Drillhole	1	15	Tertiary
Baumiller and Bitner, 2004	*Argyrotheca cuneata*	Drillhole	24	15	Tertiary
Bitner, 2000	*Argyrotheca vidali*	Drillhole	0.3	44	Tertiary
Simoes et al, 2007	*Bouchardia rosea*	Drillhole	0.4	0	Modern
Delance and Emig, 2004	*Gryphus vitreus*	Drillhole	1	0	Modern
Baumiller and Bitner, 2004	*Megathiris detruncata*	Drillhole	5	15	Tertiary
Baumiller and Bitner, 2004	*Megathiris detruncata*	Drillhole	4	15	Tertiary
Baumiller and Bitner, 2004	*Megathiris detruncata*	Drillhole	48	15	Tertiary
Baumiller and Bitner, 2004	*Megerlia truncata*	Drillhole	29	15	Tertiary
Baumiller et al, 2006	*Megerlia truncata*	Drillhole	34	4	Tertiary
Ruggiero, 1999	*Terebratula calabra*	Drillhole	3	3	Tertiary
Donovan, 2007	*Terebratulina palmeri*	Drillhole	3	2	Tertiary
Kowalewski et al, 1998	*Rhapidothyris beyrichi*	Drillhole	2	199	Jurassic
Hoffmeister, 2003	*Cardiarina cordata*	Drillhole	33	303	Pennsylvanian
Alexander, 1986	*Athyris spiriferoides*	Repair	1	381	Devonian
Alexander, 1986	*Cleiothyridina sublamellosa*	Repair	13	325	Mississippian
Alexander, 1986	*Composita sp.*	Repair	2	335	Mississippian
Alexander, 1986	*Composita subquadrata*	Repair	3	325	Mississippian
Alexander, 1986	*Composita subtilita*	Repair	1	297	Pennsylvanian
Alexander, 1986	*Meristina maria*	Repair	1	420	Silurian
Alexander, 1986	*Atrypa reticularis*	Repair	2	404	Devonian

Alexander, 1986	*Atrypa reticularis*	Repair	8	420	Silurian
Alexander, 1986	*Atrypa rockfordensis*	Repair	4	362	Devonian
Alexander, 1986	*Pseudoatrypa reticularis*	Repair	7	381	Devonian
Alexander, 1986	*Hebertella occidentalis*	Repair	5	451	Ordovician
Alexander, 1986	*Hebertella sp*	Repair	5	451	Ordovician
Alexander, 1986	*Onniella meeki*	Repair	4	451	Ordovician
Alexander, 1986	*Onniella meeki*	Repair	4	451	Ordovician
Alexander, 1986	*Plaesiomys subquadrata*	Repair	6	451	Ordovician
Alexander, 1986	*Plaesiomys subquadrata*	Repair	6	451	Ordovician
Alexander, 1986	*Platystrophia acutilirata*	Repair	0.4	451	Ordovician
Alexander, 1986	*Platystrophia ponderosa*	Repair	6	451	Ordovician
Alexander, 1986	*Platystrophia ponderosa*	Repair	3	451	Ordovician
Alexander, 1986	*Rhipidomella penelope*	Repair	1	362	Devonian
Alexander, 1986	*Schizophoria iowensis*	Repair	1	362	Devonian
Alexander, 1986	*Flexaria sp.*	Repair	13	325	Mississippian
Alexander, 1986	*Inflatia inflatus*	Repair	7	325	Mississippian
Alexander, 1986	*Juresiana nebrascensia*	Repair	3	297	Pennsylvanian
Alexander, 1986	*Linoproductus prattenianus*	Repair	29	297	Pennsylvanian
Alexander, 1986	*Rugosochonetes loganensis*	Repair	1	325	Mississippian
Alexander, 1986	*Lepidocyclus capax*	Repair	0.5	451	Ordovician
Alexander, 1986	*Lepidocyclus capax*	Repair	0.5	451	Ordovician
Alexander, 1986	*Sphaerirhynchia stricklandi*	Repair	5	420	Silurian
Alexander, 1986	*Homeospira evax*	Repair	2	420	Silurian
Alexander, 1986	*Hustedia sp.*	Repair	1	325	Mississippian
Alexander, 1986	*Mucrospirifer mucronatus*	Repair	0.5	381	Devonian
Alexander, 1986	*Paraspirifer bownockeri*	Repair	5	381	Devonian
Alexander, 1986	*Spirifer orestes*	Repair	1	362	Devonian
Alexander, 1986	*Spirifer pellaensis*	Repair	4	335	Missippian
Alexander, 1986	*Theodossia hungerfordi*	Repair	1	362	Devonian
Alexander, 1986	*Amphistrophia sp.*	Repair	10	420	Silurian
Alexander, 1986	*Chonetes coronatus*	Repair	8	381	Devonian
Alexander, 1986	*Derbyia crassa*	Repair	9	297	Pennsylvanian
Alexander, 1986	*Dictyoclostus sp.*	Repair	20	325	Missippian
Alexander, 1986	*Eumetria acuticosta*	Repair	2	325	Missippian
Alexander, 1986	*Hystriculina armata*	Repair	2	297	Pennsylvanian
Alexander, 1986	*Leptaena rhomboidalis*	Repair	18	404	Devonian
Alexander, 1986	*Leptaena rhomboidalis*	Repair	12	420	Silurian
Alexander, 1986	*Leptaena richmondensis*	Repair	7	451	Ordovician
Alexander, 1986	*Leptaena richmondensis*	Repair	7	451	Ordovician
Alexander, 1986	*Megastrophia concava*	Repair	33	381	Devonian
Alexander, 1986	*Neochonetes granulifer*	Repair	1	273	Permian
Alexander, 1986	*Neochonetes granulifer*	Repair	1	297	Pennsylvanian
Alexander, 1986	*Neospirifer pattersoni & N. cameratus*	Repair	4	297	Pennsylvanian
Alexander, 1986	*Orthotetes sp.*	Repair	15	335	Mississippian

Alexander, 1986	*Rafinesquina alternata*	Repair	26	451	Ordovician
Alexander, 1986	*Rafinesquina sp.*	Repair	26	451	Ordovician
Alexander, 1986	*Strophodonta demissa*	Repair	10	381	Devonian
Alexander, 1986	*Strophomena planumbona*	Repair	10	451	Ordovician
Alexander, 1986	*Strophomena sp.*	Repair	10	451	Ordovician
Alexander, 1986	*Strophonella reversa*	Repair	9	362	Devonian
Alexander, 1986	*Sulcatostrophia camerata*	Repair	3	362	Devonian
Harper, 2005	*Apletosia maxima*	Repair	10	4	Tertiary
Ruggiero, 2010	*Gryphus minor*	Repair	6	2	Tertiary
Harper, 2009	*Liothyrella uva*	Repair	4	0	Modern
Harper, 2009	*Magellania venosa*	Repair	44	0	Modern
Harper, 2009	*Magellania venosa*	Repair	28	0	Modern
Alexander, 1986	*Oleneothyris harlani*	Repair	1	60	Tertiary
Harper, 2009	*Terebratella dorsata*	Repair	23	0	Modern

CHAPTER 3

THE EFFECT OF LIMPET SHELL MORPHOLOGY ON DUROPHAGOUS PREDATION BY ADULT CANCRID CRABS

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ABSTRACT

Limpets are important prey for some crab species, yet little is known about the role of durophagy in the evolution of the limpet shell. This study aims to identify limpet shell morphologies that decrease vulnerability to durophagous predation by adult Cancrid crabs. We conducted feeding trials using three common species of Pacific Northwest limpets (*Lottia digitalis, L. pelta* and *Tectura scutum*) to assess how different shell morphologies affect mortality and handling time. We predicted that large size, shell ornament, and low-spires would result in either increased survivorship, and/or longer handling times. Mortality varied between species (G=34, *p*<0.0001): *L. digitalis* had the greatest mortality (79%, n=46), *L. pelta* was intermediate (57%, n=36), and *T. scutum* had the lowest mortality (28%, n=18). No relationship between size and resistance to predation was observed, however this may either be an artifact of insufficiently large limpets in the sample, or there may be no size refuge from adult Cancrids. Contrary to our expectation that ridges resist predation, individuals with smooth morphologies experienced significantly lower mortality (two-sided Fishers Exact F=70, *p*<<0.0001), as did those with low-spires (Kruskal-Wallis $\chi^2=14$, *p*=0.0002). As species possessing high-spires and ridges typically occur high in the intertidal where predation risk due to crabs is relatively low, these morphologies are likely adaptions to physical factors such as thermal stress.

INTRODUCTION

Durophagous crabs play an important role in shaping intertidal gastropod communities (e.g., Yamada and Boulding 1996; Burrows et al. 1999; Cannicci et al. 2002; Silva et al. 2008; Silva et al. 2010c), and morphological adaptions to predation pressure are well known in gastropods (e.g., Palmer 1977; Vermeij 1977; Bertness and Cunningham 1981; Vermeij 1983; Vermeij 1987; Dalziel and Boulding 2005). Although limpets are important prey for some crab species (Chapin 1968; Lowell 1986; Thompson et al. 2000; Cannicci et al. 2002; Silva et al. 2008; Silva et al. 2010c), and for several other shell-crushing predators (e.g., birds and fish), little is known about the role of durophagy in the evolution of the limpet shell, relative to spirally coiled gastropods. The identification of limpet morphologies that decrease vulnerability to durophagous predation could prove useful to explore the role of predation in the spatial variation of limpet abundance and diversity, this is because morphology can serve as a proxy for predation intensity (Vermeij 1987) and large-scale geographic trends in limpet morphology due to predation have

been observed; limpets in tropical regions have greater tenacities, better developed armor, and thicker shells due to increased durophagous predation (Lowell 1987; Vermeij 1987). In addition, understanding the influence of predation on limpet populations is vital, as these mollusks can be crucial in regulating algal abundance on rocky shores (Hawkins and Hartnoll 1983).

Although limpets all have conical shells with wide apertures, limpet shell morphology varies considerably across species. Several antipredatory morphologies have been proposed for limpets: size (Vermeij 1972; Hartwick 1981; Silva et al. 2008); tenacity (Vermeij 1987; Denny 2000; Silva et al. 2008); shell ornament (Lowell 1987); shell shape (Bulkley 1968; Chapin 1968; Lowell 1986); and shell thickness (Lowell 1987). Shore-level size gradients attributed to increased predation have been observed in limpets (Vermeij 1972, 1973; Hartwick 1981), and size may also provide refugia from predation if the prey size exceeds that of the maximum gape of the chela (Vermeij 1976). As limpet's primary means of defense is attachment to the substrate (Iwasaki 1993; Coleman et al. 2004; Silva et al. 2008), high tenacity is thought to be particularly important in resisting predation (Vermeij 1987; Denny 2000; Silva et al. 2008). Therefore, as large limpets require a considerably greater force to be removed from the substrate (Branch and Marsh 1978; Silva et al. 2008), they may be less vulnerable to some types of predatory attacks (e.g., prying).

Shell ornament has received very little attention in limpet predation studies (but see (Lowell 1987). In spirally coiled shells, corrugations increase stiffness preventing the shell from buckling when compressed (Boulding 1984), and strong sculptures decrease the shell surface area in contact with the crushing apparatus, restricting the application of force to the thickest parts of the shell (Vermeij 1974). However, further investigation is needed to understand whether ornament serves the same function in limpet shells. Shells with relatively low spires may be less vulnerable to durophagy, as crabs attacking low-spired ("flat") limpets are often unsuccessful in attempts to crush the shell due to difficulty finding purchase with the chela on the low-angle, sloped sides (Lowell 1986, 1987; Denny 2000). While shell thickness varies across limpet species and is not uniform throughout the shell, thicker shells can typically withstand higher and repeated loading (Boulding 1984; Boulding and Labarbera 1986).

Although biological systems may frequently be too complex for optimal foraging to apply, energy gain remains an important factor in prey selection. If we assume that predators forage optimally to maximize energy gain (MacArthur and Pianka 1966; Krebs 1977; Stephens and Krebs 1986; Clark et al. 2000; Enderlein et al. 2003), then predators will prefer prey that are the most profitable in regards to energy gained per unit handling time. Foraging crabs may select prey based on handling time either by maximizing the number of prey gained during the available foraging time, or by minimizing the time taken to acquire the prey (Elner and Hughes 1978; Rovero et al. 2000). Adult Cancrid crabs move onshore with high tide to forage, and back to deeper water during low tide due to physiological constraints (Yamada and Boulding 1996). Thus, handling time could be particularly important for adult cancrid crabs living in the shallow intertidal, as their foraging time is limited to times of submergence. Prey with morphologies that increase handling times (e.g., longer shell-breaking time or larger size) may therefore be rejected by crabs in favor of prey with shorter handling times (Boulding 1984). Shorter handling times may also serve to minimize exposure to their predators (birds, raccoons, etc.).

Here we test vulnerability of three species of common Pacific Northwest limpets *Lottia digitalis*, *Lottia pelta*, and *Tectura scutum,* to durophagous predation by *Cancer productus*. Laboratory feeding experiments were performed to determine whether differential mortality resulted from variations in limpet shell morphology: (a) large size (i.e., increased tenacity and shell thickness), (b) shell ornament (increased shell strength), and (c) low-spires (confounding crushing attacks). Morphologies that reduce vulnerability to predation should result in: (1) a smaller proportion of attack successes, and (2) longer grappling times (decreasing cost-benefit ratio, and increasing likelihood of disruption by predator).

MATERIALS AND METHODS

Predation is thought to pose a greater mortality risk for limpets than hydrodynamic forces, as the limpet shell is capable of resistance to compressive forces far in excess of pressures endured in nature due to wave action, and the shells are unlikely to ever be crushed (Cabral and Jorge 2007), or dislodged (Denny 2000) by wave action. The compressive force to crush shells of *Patella spp.* for example, ranges from 203-355 N (Cabral and Jorge 2007), while reported values of limpet tenacity for *Lottia* and *Tectura* range from 0.08-0.51 MN/m^2 (Branch and Marsh 1978;

Smith 1992; Smith et al. 1999). While the hydrodynamic forces generated by waves are typically < 0.1 MN/m^2 [see (Cabral and Jorge 2007) and references therein], such forces are not outside the range of those generated by shell crushing predators, such as crabs. For example, adult *Cancer productus* can generate crushing forces up to 264 N (Taylor 2000).

To investigate the effect of limpet shell morphology on durophagous predation by adult Cancrid crabs, laboratory feeding trials where conducted using three species of limpets (Patellogastropoda: Lottiidae) abundant in the Pacific Northwest (*Lottia digitalis*, *Lottia pelta*, and *Tectura scutum;* Figure 1). These species are morphologically distinct: the finger limpet*, L. digitalis,* is high spired, has pronounced radial ridges extending to the apex, which is located close to the anterior margin of the shell, and a small oval aperture. The shield limpet, *L. pelta,* can be either smooth or moderately ribbed at the margin, and has a high apex slightly off-center toward the anterior margin of the shell. The plate limpet, *T. scutum*, is smooth and very flat, with a low rounded apex at the center of the shell, and a large, more circular aperture. Cancrid crabs are known predators of all of these limpets (Lowell 1986), and adult *Cancer productus* forage in the intertidal zone at high tide [personal observation, (Robles et al. 1989; Yamada and Boulding 1996)]. In addition, *C. productus* has also been proposed as an important agent in structuring intertidal communities (Robles et al. 1989; Walker and Yamada 1993).

All limpets were collected from the rocky intertidal zone of False Bay on the south west shore of San Juan Island (Washington, USA). As it was not logistically feasible to remove very small limpets from the substrate without causing damage, only specimens with a length >10 mm were collected. Limpets were numbered and measured in the lab, and housed in an open circulation sea-table until employed in feeding trials. The following traditional linear measurements of the shell were taken using digital calipers (± 0.02 mm): maximum length (anterior to posterior), maximum width, and maximum height (the vertical distance from base to apex). Measurements were made before use in feeding trials due to the destructive nature of crab feeding. These measurements were chosen to capture the overall size and shape of the shell. As specimens were measured live, shell thickness could not be accurately measured due to the extension of the mantle to the edge of the interior of the shell. Limpet size, however, may also be a useful indicator of relative shell thickness, as thickness increases linearly with size (Cabral and

Jorge 2007). Shell flatness (i.e., low- vs. high-spired), was calculated as maximum height divided by maximum length. Shell length and width have also been used as accurate estimates of foot length and width in the species used here (Miller 1974; Lowell 1986). Although tenacity is affected by many factors, some of which can be difficult to measure (e.g., adhesion mechanisms), the surface area of the gastropod foot in contact with the substrate is of particular import (Branch and Marsh 1978). Tenacity, therefore, increases with foot area (Miller 1974; Smith 1992), and the surface area of the foot can serve as a proxy for tenacity. Thus, the length and width of the shell were used to calculate the base radius of the shell (Cabral and Jorge 2007) as a measure of maximum foot area:

$$\text{Base Radius} = \pi \left(\frac{\text{length} + \text{width}}{4} \right)^2$$

Ten specimens of *C. productus* were collected from various localities on San Juan Island. All crabs were starved for seven days to standardize hunger levels before being used in feeding trials, and were held in open circulation sea-tables. Water temperature in the sea-tables fluctuated between 11.9-14.2°C and salinity ranged from 28.3-31.7 ppt during the trial period. Carapace width was measured between the tips of the anterolateral spines using digital calipers, and crabs ranged in size from 8.6-12.4 cm (no small or juvenile crabs were used). In addition, as chela height is closely correlated with crushing strength (Boulding 1984), chela height of the dominant claw was also measured. Previous studies examining the effects of crab predation on limpets used small and juvenile crabs (Silva et al. 2008), which typically forage in the upper-middle intertidal (Yamada and Boulding 1996). However, predation pressure is expected to be highest in the lower intertidal (Vermeij 1972) where larger, adult cancrid crabs forage during submergence (Robles et al. 1989; Yamada and Boulding 1996). Thus, only large, adult crabs (most likely instar 11-13) were used in this study to assess the effectiveness of prey commonly encountered by these predators.

To ensure that all crabs were offered similar prey, limpets were allocated to one of two size categories (small and large) based on species-specific maximum length: *L. digitalis* – small <15 mm, large >15 mm; *L. pelta* – small <20 mm, large >20 mm; *T. scutum* – small <17 mm, large >17 mm. All limpets were examined for evidence of damage (e.g., chipped shells), and only

robust, undamaged individuals were retained for feeding trials. In each trial ten limpets from each species (five small and five large individuals) were randomly placed on two similarly sized submerged rocks in a sea table, and allowed to acclimatize for six hours to fully restore tenacity after relocation. One crab was then placed in the sea table with the prey, and observed for one hour after feeding behaviors ceased; crabs were not fed between trials. *C. productus* is most active at night, and it was assumed that the spectral sensitivity maxima of this dark-adapted crustacean is ~500 ±15 nm (Goldsmith and Fernandez 1968; Cronin and Forward 1988). Therefore, to minimize disturbance, feeding trials were conducted at night under red light, which does not transmit wavelengths between 420-520 nm. If a crab consumed all thirty limpets, it was presented with another set of thirty, and monitoring continued; in this case, all data collected were considered a single feeding trial. During feeding trials each individual attack was directly observed: the identity of the limpet was noted, the attack was timed, and attack strategies were described. Grappling and handling times were recorded to the nearest second using a digital timer. Grappling refers to the time from the onset of the attack to either the start of consumption, or the cessation of the attack. Handling refers to the total time of the predatory encounter, i.e., from the onset of attack to the end of consumption, not including digestion (note that handling includes grappling time, and that failed attacks therefore result in handling time equal to grappling time). Crabs are known to utilize several attack strategies (Lowell 1986), therefore crab attack behaviors were also described and recorded for each attack.

Each feeding trial thus resulted in a variety of data about both predator and prey. For every individual limpet attacked, the following were recorded (Appendix C): (1) prey species; (2) maximum length, width and height of the prey shell, from which maximum foot area (tenacity) can be calculated; (3) grappling time; (4) handling time; (5) all attack strategies employed by predator; (6) the outcome of each attack strategy employed during the encounter; and (7) the ultimate outcome of the encounter (mortality or survival). All linear measurement data were log transformed before statistical analyses, which were performed using the statistical software package SAS 9.2 (SAS Institute, Cary, NC). Statistical analyses were used to determine whether potentially antipredatory shell characteristics such as size, shape, tenacity or ornamentation resulted in lower mortality, or longer grappling and handling times. A predatory encounter with an individual limpet will ultimately result in mortality or survival, however during the encounter,

multiple attack strategies may be employed by the predator. Therefore, when considering differential survival, only the ultimate outcome of an encounter is considered (i.e., survival or consumption), while in analyses utilizing attack strategies, each strategy employed during an encounter has an outcome and is considered an observation.

To determine the effects of limpet shell morphology on durophagous predation, we tested the following hypotheses: (1) Differential mortality will occur due to some (or all) of the following differences in shell morphology, (a) large size (increased shell thickness, increased tenacity, and exceeding maximum gape), (b) shell ornament (increased shell strength), and (c) low-spires (difficulty finding purchase). Morphological characteristics that are antipredatory should result in either lower mortality, or longer handling/grappling times. (2) If crabs select prey to maximize net energy gain, then crabs will preferentially attack large limpets. (3) Crabs will utilize different attack strategies based on prey morphology, and success will vary across strategies.

RESULTS

Prey Size

Individuals in both the "small" and "large" size categories (see Methods) were attacked in similar proportions (Table 3; small n=85; large n=100), and mortality between small and large limpets did not differ overall (two-sided Fisher's Exact F=0.1, p=1), or within species (Chi-square; *L. digitalis*, p=0.70; *L. pelta*, p=0.82; *T. scutum*, p=0.31). Neither grappling nor handling time differed significantly between the small and large prey size categories (Kruskal-Wallis χ^2=0.06, p=0.79; Kruskal-Wallis χ^2=0.2, p=0.63).

Mean base radius of the shell (maximum foot surface area) did not differ between limpets that survived attacks, and those that were consumed overall (Kruskal-Wallis χ^2=3.1, p=0.07), nor within species in a two-way analysis of variance (*L. digitalis*, p=0.66; *L. pelta*, p=0.57; *T. scutum*, p=0.61). The base radius of the shell was significantly correlated with grappling time (r=0.14, p=0.04) and handling time (r=0.21, p=0.003), but not with chela height (p=0.99). Shell height was correlated with base radius (r=0.6, p<0.0001).

Shell Ornament

Mortality differed between smooth and ribbed individuals (two-sided Fishers Exact F=70; $p<<0.0001$). Smooth limpets experienced lower mortality than ribbed forms (Table 3; 41% and 78% respectively), and were more frequently attacked (64%). Mean grappling time varied significantly with attack success (Kruskal-Wallis $\chi^2=5$, $p=0.02$), and between ribbed and smooth individuals (Kruskal-Wallis $\chi^2=14$, $p=0.0001$). Mean handling time also varied between ribbed and smooth individuals (Kruskal-Wallis $\chi^2=7$, $p=0.02$).

Height-Length Ratio

Mortality differed significantly between low- and high-spired forms (Kruskal-Wallis $\chi^2=14$, $p=0.0002$), and the mean height-length ratio for failed attacks was smaller (i.e., flatter with lower-spires; Figure 2). Neither grappling time nor handling time were correlated with flatness ($p=0.5$; $p=0.7$).

Attack Strategies

Crabs utilized three main attack strategies when preying on limpets, (*sensu* Lowell 1986): (1) apex crushing, (2) marginal crushing, and (3) prying. Crushing entails the scissor-like application of force with the chela at either the apex or margins of the shell. When successful, apex crushing destroys the upper portion of the shell, while marginal crushing can either chip the shell edge, or if successful, fracture the shell. Prying involves the insertion of the walking legs (or in rare cases the chela) under the edge of the shell, levering the limpet from the rock surface. Although prying attacks resulted in shells being detached whole (undamaged), these shells were subsequently broken via manipulation during feeding. Feeding crabs held the shell with both chelae in front of the mouth to eat out of the shell, often either twisting the chela in opposite directions and "tearing" the shell into smaller pieces, or pulverizing the apex and central portion of the shell with the mouth apparatus as a consequence of feeding, leaving a characteristic hollow ring comprised of the shell margin (which is usually thicker in limpets). Thus, shell remains typically consist of small shell fragments regardless of attack strategy, due to the destructive nature of crab feeding.

Multiple attack strategies were commonly used by crabs when attacking an individual prey item. Note that in the analysis of the frequency and success of attack strategies, an attack on an individual prey consists of multiple attack strategies each considered an observation. Trials therefore resulted in the observation of 249 attacks (Table 2). Prying was observed in 82% of attacks (n=179), followed by edge crushing in 25% (n=62), and apex crushing in 3% (n=8). Nearly half of prying attacks succeeded (45%). In contrast, a larger proportion of edge crushing attacks resulted in failure (69%; n=43). As only eight attacks utilized apex crushing, these strategies were subsequently excluded from statistical analyses. Proportions of prying and edge crushing attacks did not vary significantly across limpet species (χ^2=1.47, p=0.47). Overall, prying resulted in mortality significantly more frequently (χ^2=3.85, p=0.04) in comparison to edge crushing. Within species, comparison of mortality due to edge prying versus crushing did not differ significantly for *L. digitalis* (χ^2=2.02, p=0.15) or *T. scutum* (χ^2=0.13, p=0.72), but did for *L. pelta* (χ^2=4.42, p=0.03) where edge crushing attacks had the lowest proportion of mortality (30%).

DISCUSSION

While mortality did not differ between small and large limpets, handling and grappling time increased with base radius. If base radius is an accurate approximation of tenacity, large limpets may require a disproportionate increase in energy costs along with the caloric benefits, as tenacity increases with size. Although prey size is thought to be important in predator selection, as larger prey often represent a larger net energy gain (relative to cost), this may not be the case for limpets. Large crabs should be able to handle larger prey, as both chela strength and gape increase with crab size (Boulding 1984), and should have a corresponding higher attack success rate than smaller juveniles, based on mechanical advantage. Limpet size and tenacity may, therefore, be irrelevant in determining the outcome of attacks when considering mortality due only to adult Cancrids. Other factors such as shell failure may also be more important than tenacity, as once the shell fails, tenacity is irrelevant. These findings reinforce the importance of small and juvenile crabs in limpet mortality, as crushing attacks on small limpets appear to be more frequently employed by juvenile crabs (Silva et al. 2010a; Silva et al. 2010b). Alternatively, base radius may not be a good measure of tenacity which may be dependent on features not measured here, such as the area of muscle attachment, foot flexibility, number of mucocytes, and mucus secretion (Branch and Marsh 1978).

Although radial ridges may strengthen the limpet shell, there was no evidence that the presence of ridges decreased mortality or increased handling time. Conversely, smooth morphologies experienced lower mortality and longer grappling times, confounding crushing attacks through crabs inability to find purchase with the chela on the sides or edges of the shell. A larger time investment by the predator results in lower profitability of smooth individuals, and increases exposure to their own predators. Although it is possible that ridges strengthen the edge of the limpet shell (as suggested by Lowell 1986), it seems unlikely that ridges are capable of increasing shell strength enough to deter crabs. Our observations suggest that if crabs obtain purchase either on the slopes or edges of the shell with the chela, and the gape is sufficient, they are easily capable of generating crushing forces sufficient to break the shell. This is also consistent with our observations that low-spired limpets experience lower mortality.

Crabs are typically thought of in terms of their impressive ability to crush. They do, however, commonly employ other attack strategies such as shell peeling (spirally coiled gastropods) or prying (limpets). In order for an antipredatory adaption to evolve, it must not only increase survivorship, but the type of predatory encounter must also occur frequently. Although prying was the most commonly observed attack strategy, survival and mortality occurred in nearly equal proportions. Adaptations that reduce the success of prying attacks may, therefore be important in regards to predation by juvenile cancrids and omnivorous crabs that are unable to crush limpet shells. Juvenile crabs have smaller gapes and crushing capabilities, as do some omnivorous crabs whose chelae are not specialized for crushing, and are known to incorporate a substantial proportion of limpets in their diet (Cannicci et al. 2002).

Mortality was greatest for the high-spired *L. digitalis*, which also has pronounced radial ridges, and this species is thus most vulnerable to crab predation. However, *L. digitalis* is found high in the intertidal, and individuals of this species therefore experience less immersion time. As adult *C. productus* only forage during submergence, predation in the upper intertidal is less intense, essentially providing a refuge for *L. digitalis*. Limpets living lower in the intertidal, such as low-spired and smooth *T. scutum*, appear to be better adapted to survive durophagous predation by crabs, while species living high in the intertidal, such as tall and ribbed *L. digitalis*, may be

better adapted to desiccation as tall-spires and ridges reduce thermal stress (Harley et al. 2009). This is consistent with the observation that mortality higher on the shore is due mainly to physical factors (temperature, desiccation, salinity, etc.), while mortality in the lower intertidal is predominantly the result of predation and other biotic interactions (Vermeij 1972).

CONCLUSIONS

Of the limpet morphologies examined here, low-spires and smooth shells appear to be antipredatory adaptions to durophagous predation. Our observations of crab attack behavior suggest that large size and greater shell edge thickness may also be important in increasing survivorship. Although radial ridges may strengthen the edge of the shell, we found no evidence that their presence decreases mortality in respect to predation by adult Cancrids. Individuals with high-spires and ridges are typically found on species living high in the intertidal where predation risk due to crabs is relatively low, and are adaptions to physical factors such as thermal stress.

ACKNOWLEDGMENTS

FIGURES AND FIGURE CAPTIONS
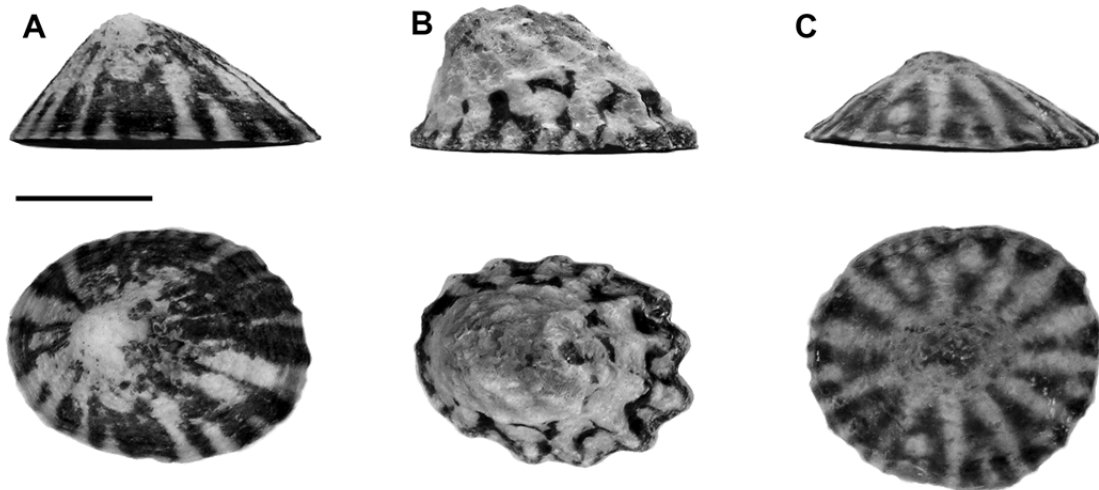
Figure 1. Three species of Lottiidae limpets from False Bay, San Juan Isl., WA: (A) *Lottia pelta,* **(B)** *Lottia digitalis* **and (C)** *Tectura scutum***. Top row is a lateral view; second row shows a dorsal view. Scale bar (1 cm).**
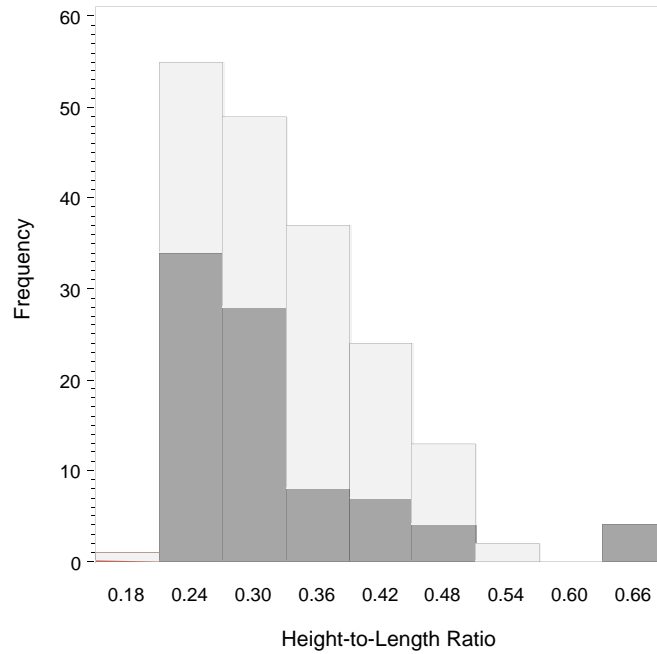
Figure 2. Flatness (Height-to-length Ratio) and differential mortality. Mortality is lower when limpets are low-spired (i.e., have a smaller height-to-length ratio), with a noticeable increase in survival when the height-to-length ratio is less than 0.36. Although flatness was binned in 0.06 increments, the pattern remains similar regardless of bin size. Dark grey denotes survived attacks, light grey denotes mortality.

TABLES AND TABLE CAPTIONS

Table 1. Attack outcome across species. Although species were attacked in equal proportions, the outcome of attacks was not uniform across species. For example, 79% of attacks on *L. digitalis* were successful, while only 28% of attacks on *T. scutum* succeeded (Likelihood=34; *p*<0.0001)

	L. digitalis	*L. pelta*	*T. scutum*	Total
Survived	12 (21%)	27 (43%)	46 (72%)	**85 (46%)**
Mortality	46 (79%)	36 (57%)	18 (28%)	**100 (54%)**
Total	**58 (31%)**	**63 (34%)**	**64 (35%)**	**185**

Table 2. Attack strategy and outcome, within and across species. S=survived; M=mortality; %= mortality due to strategy (mortality divided by total observations within species). Apex crushing was only observed eight times, however this behavior was employed by three of the nine crabs. Mortality varied across strategies (Likelihood=7; *p*=0.03), and although prying attacks comprised the most common attack strategy, edge crushing attacks had the lowest proportion of mortality (31%).

	Prying			Apex Crushing			Edge Crushing			
	M	**S**	**%**	**M**	**S**	**%**	**M**	**S**	**%**	**Total**
L. digitalis	36	14	52	1	1	1	9	8	13	**69**
L. pelta	32	36	34	0	6	0	4	15	4	**93**
T. scutum	12	49	14	0	0	0	6	20	7	**87**
Total	**80**	**99**	**-**	**1**	**7**	**-**	**19**	**43**	**-**	**249**

Table 3. Mortality by prey size and ornament. Both small and large limpets were attacked in similar proportions (45% and 54% respectively), and mortality between the two size groups did not differ (two-sided Fisher's Exact F=0.1, *p=1*). *L. digitalis* – small ≤15 mm, large >15 mm; *L. pelta* – small ≤20 mm, large >20 mm; *T. scutum* – small ≤17 mm, large >17 mm. Smooth individuals were attacked more frequently than ribbed individuals, and of the 118 smooth limpets attacked, 59% survived the encounter, while only 22% of the 67 ribbed individuals survived a predatory encounter (two-sided Fisher's Exact F=70; *p<<0.0001*).

	Survived	Mortality	Total
Small	39 (46%)	46 (54%)	85 (46%)
Large	46 (46%)	54 (54%)	100 (54%)
Smooth	70 (59%)	48 (41%)	118 (64%)
Ribbed	15 (22%)	52 (78%)	67 (36%)

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APPENDIX C

MORPHOLOGICAL MEASUREMENTS AND
ENCOUNTER DATA

Prey Species	Length (mm)	Width (mm)	Height (mm)	Foot Area	Ribs	Grap. Time (s)	Hand. Time (s)	Result	No. Attack Strat.
Lottia digitalis	21.0	17.0	6.0	280	1	426	.	S	1
Lottia digitalis	11.5	8.7	4.1	79	1	7	79	M	1
Lottia digitalis	13.9	9.1	5.8	99	1	31	.	S	1
Lottia digitalis	13.9	9.1	5.8	99	1	3	69	M	1
Lottia digitalis	13.9	9.2	5.6	100	1	1	20	M	1
Lottia digitalis	15.3	11.2	5.3	135	1	4	48	M	1
Lottia digitalis	16.4	12.6	6.4	162	1	1	90	M	1
Lottia digitalis	17.3	12.3	6.7	167	1	4	30	M	1
Lottia digitalis	20.7	15.8	8.0	257	1	16	150	M	3
Lottia digitalis	11.5	8.2	6.5	74	1	2	15	M	1
Lottia digitalis	14.9	10.5	6.1	123	1	10	78	M	1
Lottia digitalis	15.0	12.0	5.5	141	1	5	59	M	1
Lottia digitalis	17.5	12.1	6.9	166	1	3	79	M	1
Lottia digitalis	18.1	13.9	6.9	198	1	4	106	M	1
Lottia digitalis	18.7	13.6	8.5	200	1	6	92	M	2
Lottia digitalis	15.6	12.8	5.4	157	1	79	.	S	2
Lottia digitalis	12.1	8.6	4.5	82	1	93	.	S	1
Lottia digitalis	12.1	8.6	4.5	82	1	2	.	S	1
Lottia digitalis	12.5	9.3	4.5	91	1	2	54	M	1
Lottia digitalis	12.7	9.0	4.2	90	1	11	80	M	1
Lottia digitalis	13.0	9.5	4.0	97	1	8	25	M	1
Lottia digitalis	13.6	9.0	6.4	96	1	1	126	M	1
Lottia digitalis	15.8	11.2	6.3	139	1	7	132	M	1
Lottia digitalis	16.4	11.0	6.6	142	1	5	164	M	1
Lottia digitalis	17.3	12.9	6.2	175	1	1	278	M	1
Lottia digitalis	18.6	15.8	7.3	231	1	8	321	M	1
Lottia digitalis	18.9	13.3	7.1	197	1	1	125	M	1
Lottia digitalis	10.2	6.7	4.9	54	1	28	58	M	3
Lottia digitalis	11.9	8.9	3.9	83	1	26	80	M	2
Lottia digitalis	14.9	10.4	6.4	122	1	5	.	S	1
Lottia digitalis	14.9	10.4	6.4	122	1	19	.	S	1
Lottia digitalis	14.9	10.4	6.4	122	1	17	54	M	1
Lottia digitalis	15.7	10.9	7.2	134	1	8	.	S	1
Lottia digitalis	15.7	10.9	7.2	134	1	8	.	S	1
Lottia digitalis	15.7	10.9	7.2	134	1	3	.	S	1
Lottia digitalis	15.7	10.9	7.2	134	1	7	.	S	1
Lottia digitalis	15.7	10.9	7.2	134	1	20	123	M	3
Lottia digitalis	16.9	12.5	7.3	166	1	2	54	M	1

Lottia digitalis	17.9	12.2	6.9	172	1	11	51	M	1
Lottia digitalis	19.1	15.2	9.0	228	1	20	94	M	1
Lottia digitalis	19.3	14.5	9.5	220	1	20	98	M	1
Lottia digitalis	11.2	7.8	4.2	69	1	2	87	M	1
Lottia digitalis	13.5	10.4	4.8	110	1	3	170	M	1
Lottia digitalis	14.4	10.3	4.5	116	1	6	100	M	1
Lottia digitalis	15.5	11.0	6.3	134	1	9	82	M	1
Lottia digitalis	15.6	12.8	5.4	157	1	13	71	M	1
Lottia digitalis	19.2	15.2	9.4	229	1	10	115	M	1
Lottia digitalis	19.5	13.8	8.9	211	1	6	135	M	1
Lottia digitalis	19.8	14.5	7.1	225	1	11	311	M	1
Lottia digitalis	14.4	10.7	5.6	121	1	6	56	M	1
Lottia digitalis	12.5	8.9	4.3	87	1	11	34	M	1
Lottia digitalis	13.0	9.7	7.3	99	1	4	74	M	1
Lottia digitalis	18.0	12.7	5.7	180	1	13	123	M	1
Lottia digitalis	13.6	10.9	5.5	116	1	18	58	M	2
Lottia digitalis	14.0	11.8	5.4	130	1	58	138	M	2
Lottia digitalis	15.0	11.1	5.8	131	1	19	75	M	1
Lottia digitalis	15.7	10.8	6.6	133	1	15	.	S	1
Lottia digitalis	18.8	14.4	7.5	213	1	14	518	M	1
Lottia pelta	19.1	15.6	4.9	234	0	2	107	M	1
Lottia pelta	24.8	21.1	8.5	411	0	66	.	S	2
Lottia pelta	24.8	21.1	8.5	411	0	37	.	S	4
Lottia pelta	40.5	30.5	16.6	970	0	3	764	M	1
Lottia pelta	15.8	11.7	5.7	145	0	24	.	S	3
Lottia pelta	15.8	11.7	5.7	145	0	12	80	M	1
Lottia pelta	17.5	14.8	4.7	203	0	13	116	M	3
Lottia pelta	20.4	16.8	5.8	269	0	34	83	M	4
Lottia pelta	22.7	19.1	5.7	341	0	14	140	M	1
Lottia pelta	24.7	20.4	12.2	396	0	11	214	M	3
Lottia pelta	27.6	23.9	7.7	518	0	20	.	S	1
Lottia pelta	27.6	23.9	7.7	518	0	27	125	M	2
Lottia pelta	43.6	38.4	14.5	1315	0	5	474	M	1
Lottia pelta	24.8	20.1	9.5	392	1	4	134	M	1
Lottia pelta	24.0	20.0	6.4	377	0	6	.	S	2
Lottia pelta	24.0	20.0	6.4	377	0	8	.	S	1
Lottia pelta	17.1	14.7	5.3	197	0	64	209	M	1
Lottia pelta	18.2	14.1	5.8	202	0	3	114	M	1
Lottia pelta	23.2	20.8	6.9	379	0	10	220	M	1
Lottia pelta	24.5	19.0	9.0	366	1	211	741	M	3
Lottia pelta	25.6	21.5	10.0	432	0	46	1649	M	1
Lottia pelta	26.1	22.6	7.8	463	0	36	585	M	4
Lottia pelta	26.9	22.7	7.5	480	0	10	.	S	1
Lottia pelta	26.9	22.7	7.5	480	0	20	.	S	1
Lottia pelta	26.9	22.7	7.5	480	0	57	.	S	1
Lottia pelta	20.0	16.0	4.9	251	0	66	.	S	1
Lottia pelta	20.0	16.0	4.9	251	0	33	83	M	3
Lottia pelta	18.3	15.7	4.5	226	0	4	82	M	1
Lottia pelta	18.4	14.0	7.0	202	1	1	100	M	1

Lottia pelta	18.5	15.3	4.4	222	0	25	.	S	1
Lottia pelta	18.5	15.3	4.4	222	0	59	172	M	1
Lottia pelta	18.8	16.6	5.1	245	0	21	.	S	1
Lottia pelta	18.8	16.6	5.1	245	0	21	89	M	1
Lottia pelta	19.2	15.8	6.4	238	0	29	182	M	1
Lottia pelta	19.9	17.3	5.3	270	0	66	.	S	1
Lottia pelta	19.9	17.3	5.3	270	0	24	143	M	3
Lottia pelta	20.1	17.5	5.2	276	0	52	134	M	3
Lottia pelta	30.2	24.8	10.1	588	0	17	.	S	1
Lottia pelta	30.2	24.8	10.1	588	0	5	179	M	1
Lottia pelta	30.6	25.6	9.2	615	0	66	313	M	1
Lottia pelta	16.4	14.4	7.2	185	0	9	.	S	1
Lottia pelta	16.4	14.4	7.2	185	0	15	64	M	1
Lottia pelta	18.8	15.7	4.8	232	0	28	64	M	1
Lottia pelta	20.0	17.3	5.6	272	0	33	247	M	1
Lottia pelta	22.0	15.4	7.4	266	1	3	.	S	1
Lottia pelta	22.0	15.4	7.4	266	1	20	344	M	3
Lottia pelta	19.8	17.0	5.5	264	0	7	.	S	1
Lottia pelta	20.0	16.2	8.3	254	1	5	.	S	1
Lottia pelta	22.9	17.1	9.4	308	1	18	.	S	2
Lottia pelta	22.9	17.1	9.4	308	1	45	208	M	1
Lottia pelta	22.0	17.2	8.0	297	1	8	93	M	1
Lottia pelta	16.8	16.3	4.0	215	0	8	.	S	1
Lottia pelta	16.8	16.3	4.0	215	0	14	.	S	1
Lottia pelta	17.7	13.2	5.4	184	0	14	.	S	1
Lottia pelta	17.7	13.2	5.4	184	0	9	61	M	1
Lottia pelta	19.0	14.4	6.6	215	0	15	80	M	1
Lottia pelta	19.8	17.0	5.5	264	0	16	.	S	1
Lottia pelta	22.5	18.0	6.0	318	0	18	181	M	1
Lottia pelta	24.1	19.5	6.7	369	0	3	241	M	1
Lottia pelta	25.3	20.8	17.3	413	0	30	.	S	2
Lottia pelta	25.3	20.8	17.3	413	0	5	.	S	1
Lottia pelta	25.3	20.8	17.3	413	0	23	.	S	1
Lottia pelta	25.3	20.8	17.3	413	0	87	.	S	1
Tectura scutum	17.6	15.1	4.7	209	0	38	.	S	1
Tectura scutum	18.7	15.7	5.6	231	0	90	217	M	3
Tectura scutum	22.8	17.9	7.2	321	0	64	199	M	1
Tectura scutum	23.7	19.8	5.6	369	0	66	335	M	3
Tectura scutum	15.5	12.3	2.8	150	0	9	73	M	1
Tectura scutum	15.6	12.7	3.8	156	0	5	46	M	1
Tectura scutum	15.8	12.7	3.6	158	0	8	72	M	1
Tectura scutum	18.5	15.6	4.7	227	0	11	137	M	1
Tectura scutum	18.8	15.8	5.1	233	0	8	.	S	1
Tectura scutum	18.8	15.8	5.1	233	0	19	.	S	3
Tectura scutum	18.8	15.8	5.1	233	0	10	56	M	1
Tectura scutum	19.7	15.8	4.8	244	0	16	54	M	1
Tectura scutum	22.7	18.8	6.1	335	0	22	90	M	1
Tectura scutum	22.7	19.1	5.7	341	0	14	72	M	3
Tectura scutum	13.3	10.8	4.2	113	0	5	.	S	1

Tectura scutum	16.5	12.6	4.0	163	0	40	.	S	1
Tectura scutum	16.8	14.5	3.8	191	0	36	.	S	1
Tectura scutum	16.8	14.5	3.8	191	0	7	.	S	1
Tectura scutum	17.2	14.7	5.0	199	0	4	.	S	1
Tectura scutum	17.2	14.7	5.0	199	0	4	.	S	1
Tectura scutum	17.2	14.7	5.0	199	0	21	.	S	1
Tectura scutum	18.7	15.1	4.3	222	0	7	.	S	1
Tectura scutum	20.0	16.3	4.8	256	0	72	.	S	1
Tectura scutum	20.0	16.3	4.8	256	0	9	.	S	1
Tectura scutum	20.0	16.3	4.8	256	0	13	.	S	1
Tectura scutum	21.3	19.3	6.1	323	0	5	84	M	1
Tectura scutum	16.8	14.1	5.1	186	0	13	92	M	1
Tectura scutum	21.8	19.5	5.1	334	0	9	168	M	1
Tectura scutum	13.9	11.7	3.7	128	0	12	.	S	1
Tectura scutum	15.4	17.7	3.4	214	0	25	.	S	1
Tectura scutum	16.1	12.5	4.5	158	0	22	.	S	2
Tectura scutum	16.1	12.5	4.5	158	0	42	.	S	1
Tectura scutum	16.3	13.4	3.9	172	0	10	.	S	2
Tectura scutum	16.3	13.4	3.9	172	0	26	.	S	2
Tectura scutum	16.3	13.4	3.9	172	0	28	.	S	2
Tectura scutum	16.3	13.4	3.9	172	0	7	.	S	1
Tectura scutum	17.5	14.8	5.0	203	0	30	.	S	1
Tectura scutum	19.3	15.9	5.5	241	0	3	.	S	1
Tectura scutum	19.3	15.9	5.5	241	0	6	96	M	1
Tectura scutum	19.7	16.3	5.0	252	0	12	.	S	1
Tectura scutum	19.7	16.3	5.0	252	0	4	.	S	1
Tectura scutum	22.6	19.6	6.4	348	0	10	.	S	1
Tectura scutum	22.6	19.6	6.4	348	0	4	.	S	1
Tectura scutum	22.6	19.6	6.4	348	0	9	.	S	1
Tectura scutum	22.6	19.6	6.4	348	0	14	.	S	2
Tectura scutum	22.6	19.6	6.4	348	0	23	.	S	1
Tectura scutum	22.6	19.6	6.4	348	0	16	.	S	1
Tectura scutum	11.7	10.0	3.0	92	0	4	.	S	1
Tectura scutum	11.7	10.0	3.0	92	0	2	.	S	1
Tectura scutum	14.2	11.3	3.6	126	0	5	.	S	1
Tectura scutum	15.0	13.0	3.5	153	0	20	.	S	3
Tectura scutum	23.7	18.8	5.4	350	0	12	101	M	1
Tectura scutum	16.3	13.4	3.9	172	0	5	.	S	1
Tectura scutum	23.5	19.3	6.0	356	0	16	.	S	1
Tectura scutum	23.5	19.3	6.0	356	0	86	.	S	3
Tectura scutum	15.0	13.0	3.5	153	0	5	56	M	1
Tectura scutum	15.3	12.5	3.4	150	0	8	.	S	1
Tectura scutum	15.3	12.5	3.4	150	0	8	.	S	1
Tectura scutum	19.0	17.1	4.6	255	0	12	67	M	1
Tectura scutum	24.0	21.4	6.8	403	0	19	.	S	2
Tectura scutum	24.0	21.4	6.8	403	0	16	.	S	2
Tectura scutum	22.6	19.6	6.4	348	0	53	.	S	1
Tectura scutum	23.5	19.3	6.0	356	0	12	.	S	3
Tectura scutum	23.5	19.3	6.0	356	0	18	.	S	1

CHAPTER 4

THE FIDELITY OF MICROSTRUCTURAL DRILLING PREDATION TRACES AND GASTROPOD RADULAR MORPHOLOGY: PALEOECOLOGICAL APPLICATIONS

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ABSTRACT

One of the major caveats of using gastropod drill holes to assess predator-prey interactions in both the modern and the ancient is the correct identification of drill holes that are of predatory origin. By examining known predator drill holes using ESEM, we hope to (1) refine the development of a novel technique for augmenting their identification, and (2) to explore the relationships between predator body size, predator dentition (radulae), and radular microrasping marks observed on the shells of prey organisms.

Drilling involves the intermittent use of the accessory boring organ and the radula, which physically rasps away shell material leaving microtraces within the drill hole. Variation in the spacing of these rasping microtraces may be due to the radular intercusp spacing, as well as the overprinting of multiple radular passes. In an effort to confirm that microtraces observed in drill holes are the result of radular rasping and not an artifact of crystalline shell microarchitecture, both radular rasp marks and drill holes were artificially replicated and examined using environmental scanning electron microscopy. Examination of the size and morphology of replicated radular rasp marks indicates high fidelity between rasp marks and predator dentition. In addition, microtraces were not present in artificially drilled holes in *Mytilus edulis* shells. Microtraces are therefore interpreted as drilling predation microtraces produced by predator radulae.

Feeding experiments performed at Friday Harbor Laboratories (San Juan Isl., WA) yielded 35 drilled mussel shells and the radulae extracted from their corresponding predators (*Nucella lamellosa*). The spacing between microtraces observed in drill holes correlates with intercusp spacing of the radulae extracted from the individual responsible for drilling ($p=0.03$). Microtraces of drilling predation may therefore serve as an estimate of radula size. Intercusp spacing, however, did not correlate with gastropod shell height thus radula size is not an accurate proxy for predator size and cannot be inferred from microrasping traces.

Drilling microtraces provide an additional tool for the identification of traces of predation in the fossil record, and reveal novel research avenues for studies investigating predation in fossil record where the predator's identity may be unknown.

INTRODUCTION

Drill holes in prey skeletons provide direct evidence of predator-prey interactions. Due to their preservation in the fossil record, these traces have been used to examine predation on a variety of spatial and temporal scales including predation intensity through time (Vermeij 1977; Vermeij 1987; Leighton 2002; Huntley and Kowalewski 2007), spatial variation in predation (Vermeij et al. 1980; Hansen and Kelley 1995; Hoffmeister and Kowalewski 2001), timing of diversification and evolution of species (Kase and Ishikawa 2003), and interspecies prey selectivity (Kelley and Hansen 1996). While drill holes are widely used to investigate both ancient and modern predation, the recognition and verification of predatory origin can still be contentious, despite well-established criteria (see Kowalewski 2002). Specifically, issues remain in distinguishing traces that are predatory in origin from those formed by either other biotic or abiotic means, such as domicile or parasitic holes, dissolution or bioerosion, and non-predation punctures (Lescinsky and Benninger 1994; Kaplan and Baumiller 2001; Wilson and Palmer 2001; Kowalewski and Kelley 2002; Kelley et al. 2003).

Recent efforts to augment our ability to accurately identify the origin of drill holes aim to establish a set of microstructural criteria (Schiffbauer et al. 2008). This microstructural work was based on a basic, but fundamental, assumption: extraction of a substrate by a mechanical process should leave recognizable tool marks associated with the instrument used for material removal. Evidence for these tool marks have been previously reported for both modern prey-shell drilling by gastropod predators (Carriker 1969; Carriker et al. 1974; Carriker et al. 1978; Schiffbauer et al. 2008), as well as *Radulichnus* pendulum grazing structures observed deep in the molluscan evolutionary tree associated with the Ediacaran fossil *Kimberella* (Seilacher 1999). The microscale radular traces associated with drill holes of predatory origin consist of rasp marks exhibiting a corrugated texture produced by the mechanical scraping of the radula. The distance between the tips of the radula cusps is thought to correspond with the interval between the parallel rasp traces produced by a stroke of the radula (Carriker 1969). These microtraces can be recognized under high magnification scanning electron microscopy (SEM), and have been observed within drill holes of a wide range of prey species including limpets, mussels, and clams (Carriker 1969; Carriker et al. 1974; Carriker et al. 1978; Schiffbauer et al. 2008). Initial observations of radular rasp marks, however, have been limited to incomplete drill holes, and

descriptions of rasp marks within complete drill holes are lacking (but see Schiffbauer et al. 2008). Relative to the initial characterizations of radular rasp marks made on the relatively flat base of incomplete drill holes (Carriker 1969; Carriker et al. 1974; Carriker et al. 1978), the morphology of rasp marks on the sloping walls of a complete drill hole are more complex. Here successive marks may not be erased by the chelating secretions of the accessory boring organ (as is the case with those observed on the base of incomplete holes), and multiple strokes are often evident (Schiffbauer et al. 2008). Previous analyses describing the morphology of these microtraces were unable to conclusively eliminate the alternative hypothesis that microtraces along the drill hole walls are an artifact or expressions of crystalline microarchitecture of the shell, even though features attributed to the mechanical rasping of the radula and those of crystalline shell structure are at different, but slightly overlapping scales (Schiffbauer et al. 2008).

To date, no attempts have been made to determine the utility of drilling microtraces in extracting biological information, such as the size of predator. It would be advantageous if additional information regarding the identity or size of the predator could be extracted from drilling microtraces, as direct observations of gastropod predatory behavior can be time consuming, logistically difficult, or impossible to obtain. Thus, in addition to refuting the hypothesis that traces are simply a function of shell microstructure, the relationship between microtrace morphology and radula morphology has not been quantitatively characterized yet.

To further our understanding of the relevance and utility of drilling predation microtraces, this study aims to (1) replicate microtraces to confirm that traces are indeed the result of radular rasping, and not simply shell crystalline microarchitecture, and (2) explore the utility of extracting additional biological information from drilling predation microtraces by both evaluating the morphological fidelity of radular rasp marks relative to predator dentition, and determining whether drilling microtraces can serve as a proxy for predator size. The characterization of radular rasp marks could be of particular importance in paleontological studies where the identity of the predator is often uncertain, or the predator population is not preserved in the assemblage.

DESCRIPTION OF THE DRILLING PROCESS

Murician radulae consist of several hundred rachidian teeth in transverse rows forming three longitudinal rows of teeth supported on a radular membrane (Figure 1 A-C), and are housed within the buccal mass at the end of the proboscis, supported on the tongue-like odontophore within the buccal cavity. These radulae are rachiglossan, and each transverse row of teeth consists of a more robust rachidian, or central cusp, and two marginal cusps (Carriker 1981). Muricid gastropods bore a cylindrical hole through the shell of the prey through which they extend the proboscis to feed. Holes are bored using the radula to remove material through mechanical scraping, in alternation with the application a chelating agent via the accessory boring organ (ABO), which chemically weakens the shell structure. During drilling, the odontophore extends ventrally from the mouth towards the substrate, and once in contact with the surface of the shell, is drawn forward in a "licking" motion, scraping the cusp points across the chelated shell surface (Carriker 1969). At the end of the rasping stroke, the odontophore is pulled back into the buccal cavity where shell material is swallowed. A single rasping stroke employs several transverse rows of teeth, from 14-34 rows (Carriker et al. 1974). The unfolding of the radula is such that only the central rachidian teeth typically come into contact with the shell surface and marginal teeth are predominantly employed in feeding (Carriker 1969). However, drilling observations indicate that the odontophore may be oriented either straight relative to the substrate, or held slightly to one side, causing the rachidian cusp and one of the lateral cusps to scrape simultaneously (Carriker 1969). The radula, therefore, may scrape from one side of the borehole to the other, at right angles, or follow the circumference of the hole (Carriker 1969).

As rasping activity decreases during the drilling process, the radula plays a considerable role in the early stages of drilling (3,000 to 500 rasps), and is responsible for a large portion of shell penetration (Rovero et al. 1999). Drilling may take anywhere from 50-150 hours (Radwin and D'Attilio 1976) depending on the thickness and composition of the prey shell. Each rasping stroke leaves conspicuous parallel scrapes on the shell, and rasp traces can consist of either one trace, or several parallel grooves. The distance between the tips of the cusps is thought to correspond with the interval between the parallel cusp traces rasped in the shell, and the mechanical action of rasping accounts for the removal of approximately 10-20% of the shell material (Carriker 1969).

MATERIALS AND METHODS

Mechanical Microtrace Replication

To assess the alternative explanation, i.e., that the *Radulichnus*-like microtraces observed within complete drill holes could be an expression of crystalline shell microarchitecture, we performed two mechanical tests: (1) radulae extracted from *Nucella lamellosa* (Gmelin) (Muricidae, Ocenebrinae) were scraped across wax substrates to mimic the structures produced by natural radular rasping action. The sizes and morphologies of the resultant traces were then directly compared to observed microtraces on prey shells; (2) Holes were artificially drilled in shells of *Mytilus edulis* (Linnaeus) (Mytilidae) with a common drill bit to determine whether microtraces were visible in *any* drilled hole, regardless of the means of production. If rasp marks created on the wax substrate were not comparable to the observed microtraces interpreted as produced by the radulae of drilling predators, or microtraces were indeed present on the walls of artificially drilled holes, then microtraces may simply be an expression of crystalline shell microarchitecture.

For the mechanical reproduction of microstructures using extracted radulae, we utilized an integrated OmniprobeTM tungsten micromanipulator probe needle housed within an FEI Company DualbeamTM Helios 600 NanolabTM focused-ion beam electron microscope (FIB-EM; Schiffbauer and Xiao 2009, 2011). After carefully looping the <0.5 µm diameter probe tips to provide a sturdier base, radulae extracted from *Nucella lamellosa* were affixed using superglue and the probe tip was inserted into the micromanipulator (Figure 1 D). Pure beeswax was applied to the surface of a standard aluminum SEM stub, and then sputter coated with 5 nm of gold-palladium. Because the beeswax was melted onto the surface of the SEM stub, it provided a smooth substrate for mechanical generation of rasp marks. Under live secondary electron imaging (at an electron beam accelerating voltage of 1 keV, beam current of 86 pA, and a working distance of 4.1 mm), the micromanipulator probe with attached radula was carefully positioned and dragged across the surface of the wax-coated stub with sub-µm-scale control. The resulting artificial rasp marks were then perpendicularly cross-sectioned using the gallium ion beam (at an accelerating voltage of 30 kV and current of 0.28 nA) and imaged with via secondary

electron imaging (sample surface at 142°) to directly observe the depth profile of the radula-induced traces.

To determine whether microtraces were present regardless of the drilling mechanism (i.e., in holes drilled by means other than radula rasping), holes were artificially created in the shells of *Mytilus edulis* using a 0.8 mm drill bit, and subsequently examined for the presence of microtraces using low-vacuum environmental SEM imaging (see below for detailed ESEM methods).

Microtrace Characterization

To evaluate the morphological fidelity of radular rasp marks relative to predator dentition, laboratory feeding trials were conducted so that drill holes could be produced by known individual predators, and any resultant microtraces within the drill holes could then be examined in conjunction with the apparatus that potentially produced them. If microtraces are the product of the mechanical rasping of the radula, then the interval between the parallel traces should correspond to the distance between the tips of the rachidian cusps. As microtraces consist of multiple marks, and rasping involves multiple transverse rows of teeth, the mean microtrace spacing within a drill hole was compared with the mean intercusp spacing on the corresponding predator radula. If the correlation between mean microtrace spacing and mean intercusp spacing is strong, then microtraces are likely the result of radular rasping, and serve as a good measure of the size of the radular dentition. Rasp marks could thus be used in the absence of the radula to make inferences regarding the size of the radula.

Predator size is believed to relate to drill hole diameter, as the size of the drill hole may reflect the size of the accessory boring organ (Carriker and Van Zandt 1972). Indeed, a strong correlation between predator size and drill hole size has been demonstrated for *Nucella lamellosa* (Kowalewski 2004). Furthermore, a weak correlation between radulae width and shell height was observed by Carriker and Gruber (1999). The size of the radula may, therefore, may correlate with the size of the predator. If radulae size correlates with predator size, then rasp mark spacing could be used as a proxy for predator size.

Feeding trials were conducted at Friday Harbor Laboratories (San Juan Island, WA) in October and November of 2008. Prior to utilization in feeding trials, the maximum height (from apex to aperture) of all gastropods was measured, and each gastropod numbered. All measurements were made using digital calipers (± 0.02 mm). Two open circulation sea-tables each containing 20 *Nucella lamellosa* and 18 *Mytilus edulis* (laid out in six rows of three) were observed daily over an eight week period. Once a gastropod clamped onto a mussel, initiating the drilling process, the predator and prey were isolated within the tank by encasing the pair *in situ* within a plastic mesh cage to minimize disturbance. Empty mussel shells were retrieved from the cages after feeding had ceased, the number of the gastropod was recorded and associated with the mussel shell, the mussel was replaced with a live individual, and the snail was released back into the sea-table. All gastropods that fed were collected at the end of the eight week trial and preserved in ethyl alcohol, and the resultant drilled mussels were measured, cleaned and dried. Radulae were extracted via dissection of alcohol-preserved specimens under a dissecting binocular light microscope.

To measure microtrace and radular intercusp spacing, drill holes and radulae obtained from the feeding trials were observed via secondary electron imaging under low-vacuum ESEM. All prey shells and predator radulae were analyzed in an FEI Company Quanta 600 field-emission ESEM. Secondary electron images (illustrating sample topography) were collected using a large field detector in a low-vacuum, gaseous (water vapor) chamber atmosphere, which allowed for analysis of uncoated samples (no gold-palladium or carbon coating needed). The following operating conditions were maintained through all analyses: electron beam accelerating voltage=20 keV, spot size (unit less measure of electron beam current and diameter)=5.0, working distance=11.5 mm, and chamber pressure=0.98 torr.

Prior to mounting for ESEM imaging, prey shells were agitated in an ethanol bath for a few minutes to remove any debris retained during storage. After air-drying, the shells were mounted to standard aluminum SEM stubs using conductive carbon adhesive tape. As the mussel valves were typically larger than the diameter of the SEM stubs, in each case, the shells were positioned in an effort to situate the drill hole perpendicular to the electron beam—sometimes using multiple layers of carbon adhesive to level the drill hole surface. In addition, a small strip

of carbon adhesive was applied connecting the upper surface of each shell to the stub creating a conductive bridge to aid in charge dispersal. For preparation of the radulae, following extraction, radulae ribbons were gently rinsed in distilled water and brushed with a soft-bristle paint brush to remove excess tissue. Moved directly from the distilled water bath to ensure pliability of the connective tissues holding the radular dentition, the radulae were immediately positioned on and affixed to standard aluminum SEM stubs using carbon adhesive tape and then allowed to dry prior to imaging.

Measurements assessed from secondary electron images of the radulae and microtraces were conducted using the ruler tool in Adobe Photoshop and calibrations were calculated in Microsoft Excel. The dimensions collected for analysis include the intercusp spacing on each radular tooth from the rachidian cusp to the median cusps, and the distance between adjacent microtraces located within drill holes. To maintain consistency in radular measurements, the center point of each cusp was first marked, and then the distances from adjacent cusp centers were recorded. In addition, all intercusp widths were measured perpendicular to the cusp base (see radular measurement schematic in Figure 1 C).

Statistical analyses were performed using the statistical software package SAS JMP 9 (SAS Institute, Cary, NC) to determine correlation significance between mean microtrace spacing, mean intercusp spacing, and gastropod shell height.

RESULTS

Mechanical reproduction of microstructures by scraping extracted radulae across wax substrates, created parallel grooves matching radular dentition (Figure 1 E-H), and spacing between grooves was comparable to radular intercusp spacing (Figure 1 C and E). The number and depth of the grooves created was dependent on the pressure with which the radula was scraped along the surface, and the angle of orientation relative to the substrate. Grooves made by the central rachidian cusp were typically deep and well defined. A cross section through a central groove made by a rachidian cusp (Figure 1 H) resembled rachidian cusps in size and morphology: the width of the groove generated by the central rachidian was equivalent to the width of a rachidian cusp at the corresponding level (Figure 1 I). Thus, replicated traces corresponded to the

morphology and size of the radula, and are comparable in size and structure to microtraces observed in drill holes.

Examination of the walls of mechanically replicated drill holes shows no evidence of *Radulichnus*-like microtraces (Figure 2 A-D), nor do microtraces resemble crystalline shell microarchitecture (Figure 2 E, G upper left). Replicated drill holes have smooth, uniform walls, and truncate shell crystalline microstructure visible at the shell surface (Figure 2 D).

Laboratory feeding trials resulted in 35 mussel shells drilled by 28 predatory gastropods (three predators attacked and consumed two prey each during the trial period). Microtraces were observed in 26 of the drilled holes, and 23 radulae were successfully extracted. The radula of *Nucella lamellosa,* as with other ocenebrine muricids, is a "dagger" type (Herbert et al. 2007) flattened rachidian with a more massive elongate central rachidian cusp, and weaker lateral and marginal cusps (Figure 1 A-C). Cusps are sharp and slightly hooked, curving posteriorly.

Examination of ESEM micrographs of drill hole walls revealed parallel to sub-parallel grooved marks, similar in morphology and size to those created on the wax substrates (Figure 2 G-L) in 19 drill holes (Appendix D). Microtraces also commonly cross-cut one another (Figure 2 J and K), and microtrace spacing pooled across individuals has a mean of 8.9 μm (Std. Deviation 4.1 μm), ranging from 2.3 - 30.6 μm (Figure 3 A). Radular intercusp spacing pooled across individuals has a mean of 31.9 μm (Std. Deviation 6.2 μm), and ranges from 12.5 - 50.4 μm (Figure 3 B). Mean microtrace spacing for each shell (Table 1) correlates significantly with the mean radular intercusp spacing of the predator responsible for drilling (Figure 4; Pearson's r=0.50, p=0.03), however, mean intercusp spacing does not correlate with predator shell height (Pearson's r=0.18, p=0.45).

DISCUSSION

Replication of microtraces using wax substrates confirmed that radular teeth are capable of generating parallel grooves of varying numbers and depths, on soft substrates. Overall, microtraces provide a reasonable approximation of the size of the radular dentition (i.e., intercusp spacing), and replicated traces closely resemble microtraces observed within drill holes.

Microtrace size and morphology, however, is dependent on the angle of orientation and pressure with which the radula is scraped along the surface, which may vary depending on the number of traces created in a single pass, or the width and depth of the traces.

Artificially replicated drill holes demonstrate that shell crystalline microstructure observed in cross section is typically uniform, and no *Radulichnus*-like microtraces were found in replicated drill holes. In addition, the cross-cutting observed in microtraces is an unlikely result if traces are simply an artifact of the parallel packaging of shell crystalline microstructure. Microtraces are, therefore, interpreted as radular rasp marks, and not as an artifact of shell crystalline microstructure.

Drilling predation microtraces were not observed in all drill holes examined, possibly due to the erasure of radular marks made during previous rasping periods by the secretions of the ABO (Carriker 1969). When present, radular rasp marks can be used effectively to identify predatory origins of drill holes. As microtrace spacing correlates well with intercusp spacing, radular rasp marks could be used to extrapolate intercusp spacing, provided this relationship holds true for a wide variety of radular cusp morphologies.

While rasp marks may be used to estimate the size of the radula, radular size does not appear to increase in concert with gastropod size for adult *Nucella lamellosa*. Radular rasp marks, therefore, do not serve as a proxy for predator size. The weak correlation between mean intercusp spacing and shell height may be due to physical constraints on radular size: In order for the radula to be easily maneuverable within the confines of the deepening borehole created by the ABO, an increase in the size of the radula must be accompanied by a proportional increase in the size of the ABO (Carriker and Gruber 1999).

As drilling predation microtraces are distinct from shell crystalline microstructure, and easily recognizable using high magnification imaging techniques, microtraces can be used as an additional tool to augment current methods for identifying predation traces. Examination of rasp marks produced by several other radular configurations, and including predatory gastropods from other groups (e.g., naticids), could prove a fruitful avenue for future investigations. If radular

rasp marks can be used to differentiate between predator groups on the basis of radular morphology, drilling predation microtraces could provide invaluable insights into the identity of predators in the fossil record. As drilling microtraces could prove valuable in the characterization of drill holes in contentious or degraded specimens, traces might be used to provide insight into the origins of drilling behaviors and of the radula.

Predation is considered an important force in many communities, influencing biodiversity and community structure on a variety of spatial and temporal scales (Paine 1966; MacArthur 1972; Vermeij 1977; Palmer 1979; Vermeij et al. 1980; Vermeij et al. 1981; Vermeij 1987; Hansen and Kelley 1995; Hoffmeister and Kowalewski 2001; Leighton 2002; Huntley and Kowalewski 2007). To evaluate the role of predation in evolution, however, we need effective proxies for predation pressure. Predation traces, such as drill holes and repair scars, are widely used proxies for predation intensity, as they provide direct evidence of predator-prey interactions, and are commonly preserved in prey skeletons in the fossil record (Kowalewski and Kelley 2002). Considering the utility of drill holes as proxies for predation intensity, developing novel techniques for the identification of predation traces, represents an important step in understanding the role of predation as an evolutionary force.
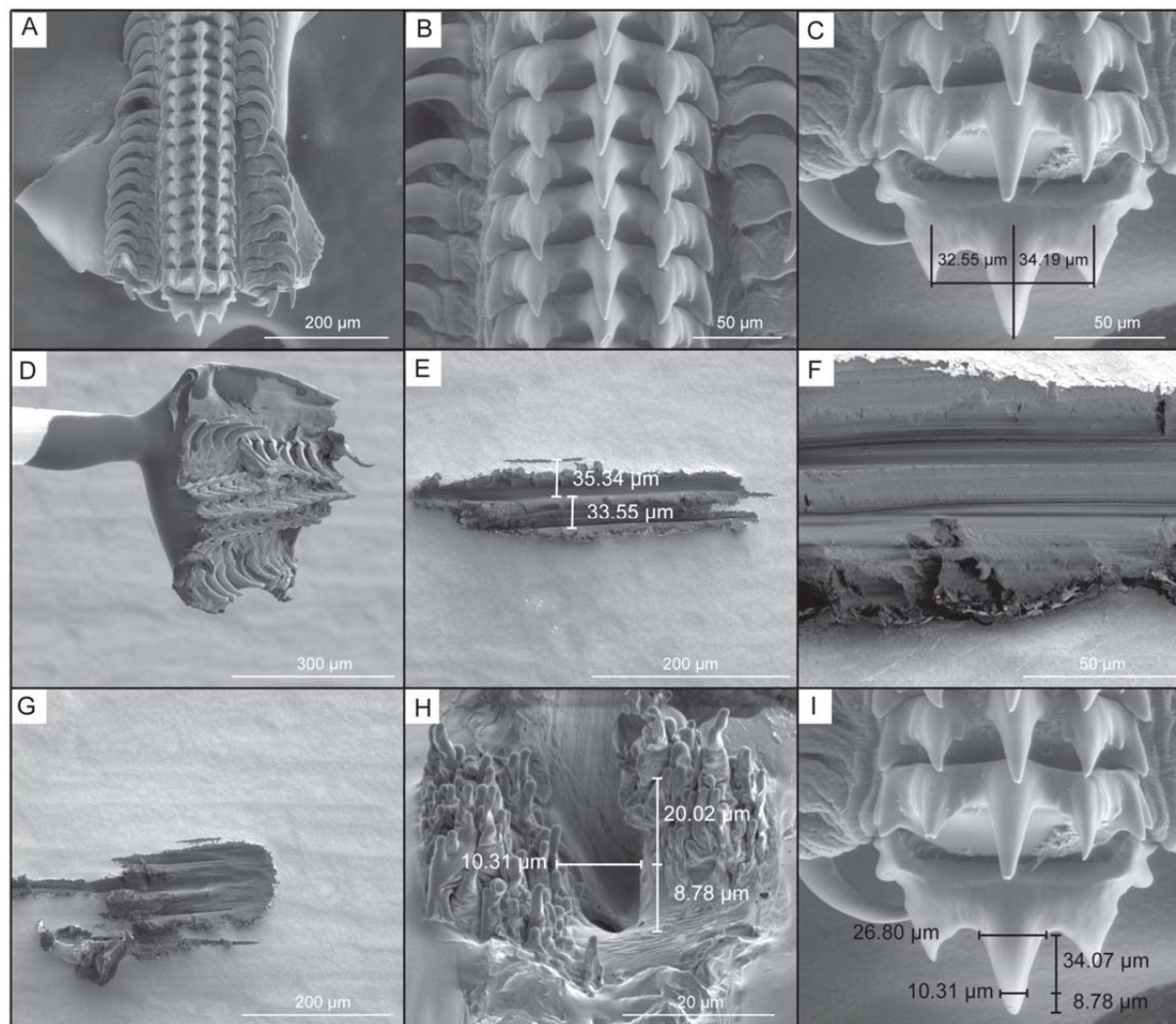
Figure 1. Representative radulae and replicate radular rasp marks. (A-C) Radulae of *Nucella lamellosa*. Portion of a radular ribbon mounted to the FIB probe tip **(D)** and used to scrape a wax substrate **(E-G)**. Spacing between grooves of replicated rasp marks **(E)** corresponds to radular intercusp spacing **(C)**. A cross section through one of the grooves **(H)** shows the fidelity of groove morphology and size, to rachidian morphology and size **(I)**. The width of the groove 8.78 μm from the base is 10.31 μm **(H)**, which corresponds to rachidian width 8.78 μm from the tip of the cusp **(I)**.
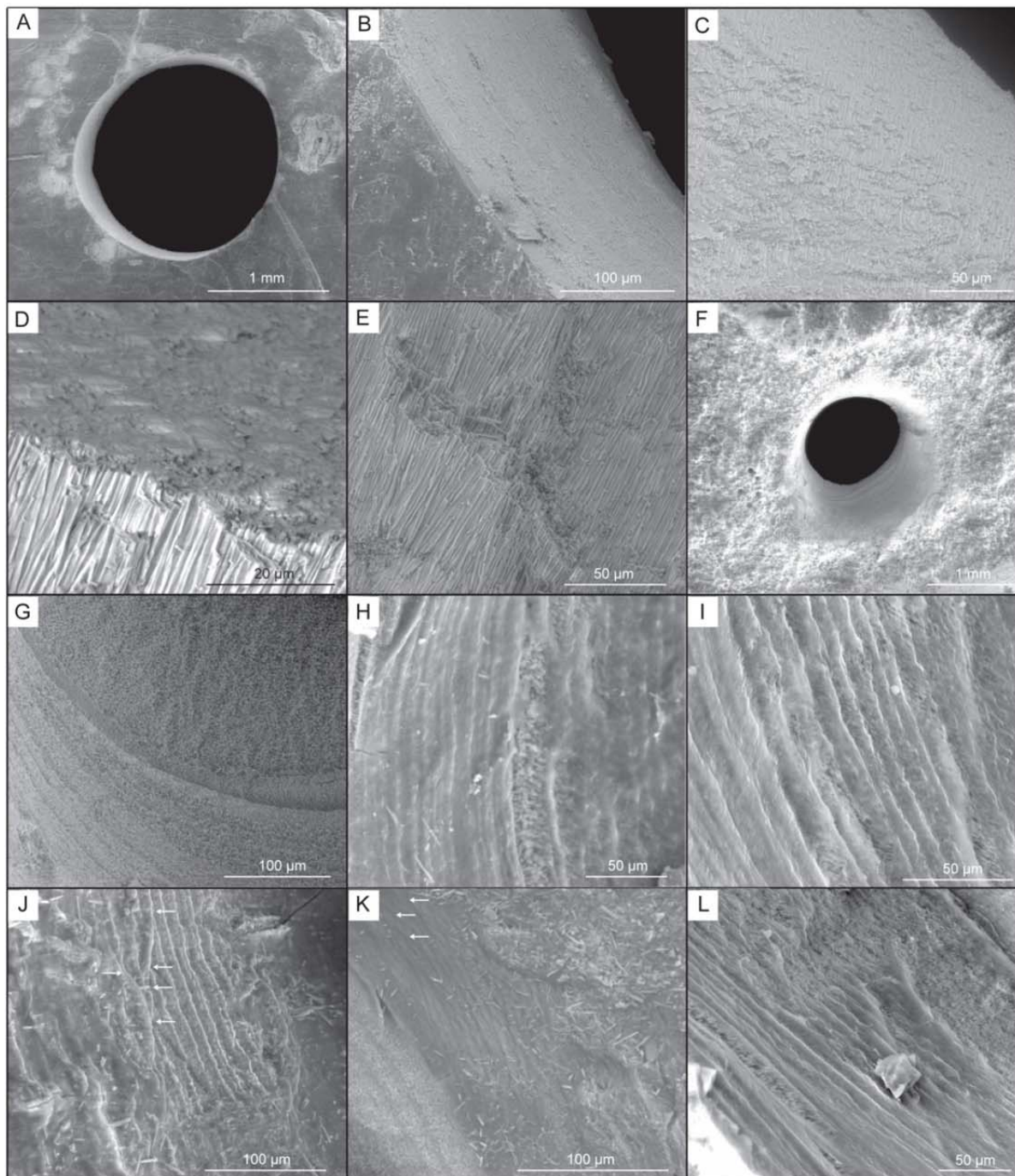
Figure 2. Representative crystalline shell microstructure and drilling predation microtraces. A-D Artificial drill hole created with a drill bit. B and C are higher magnification of the walls of the drill hole. The absence of *Radulichnus*-like microtraces along drill hole walls is apparent in B-D, and crystalline shell microstructure is visible on the shell surface in D and E, where the drill hole truncates the crystals (D). Holes drilled by *Nucella* show signs of chelation around the outer edges (F), and microtraces are visible (H-L) in contrast with uniform crystalline microstructures (G). H-L Microtraces interpreted as radular rasp marks, notice cross cutting of marks denoted by arrows in J, and K.
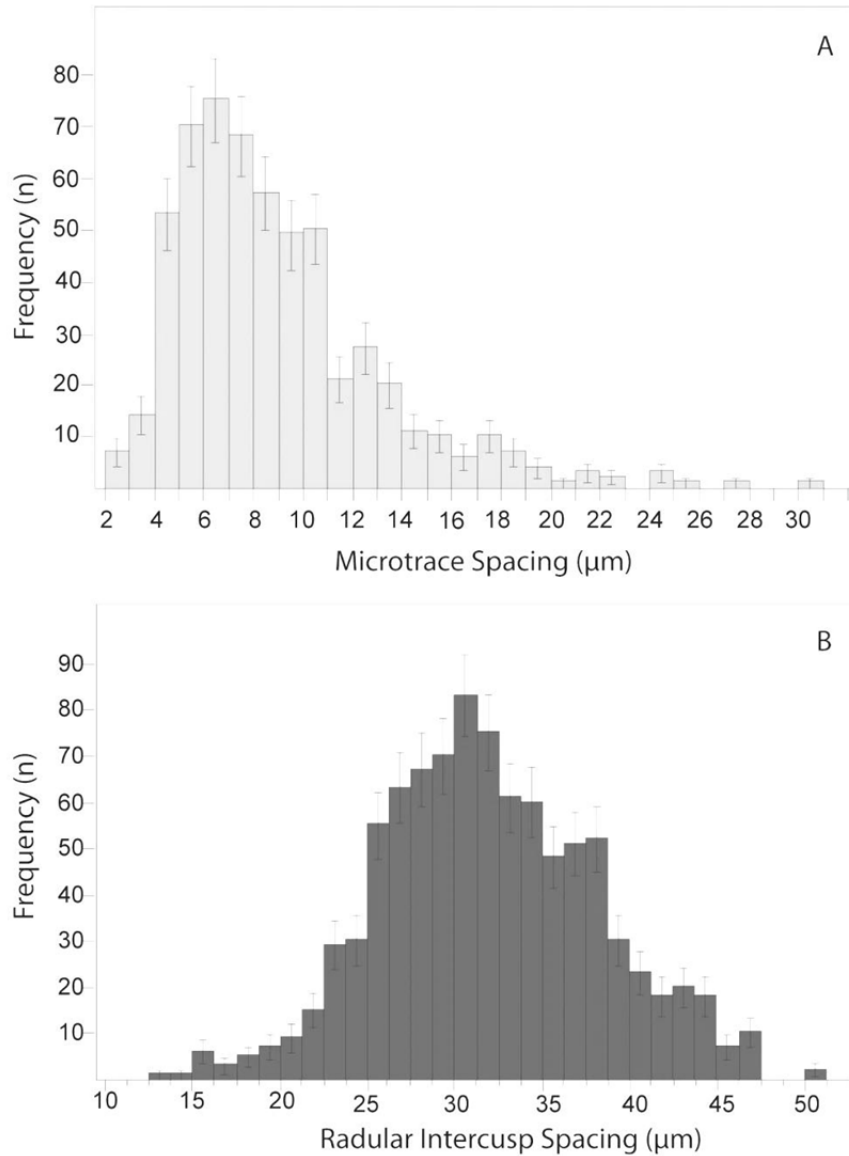
Figure 3. Frequencies of pooled microtrace and intercusp spacing. (A) Microtrace spacing in drill holes resulting from predation. (B) Intercusp spacing of radular teeth measured from gastropods responsible for drilling. Mean microtrace spacing is 8.9 μm, mean intercusp spacing is 31.9 μm, and bars are standard error.
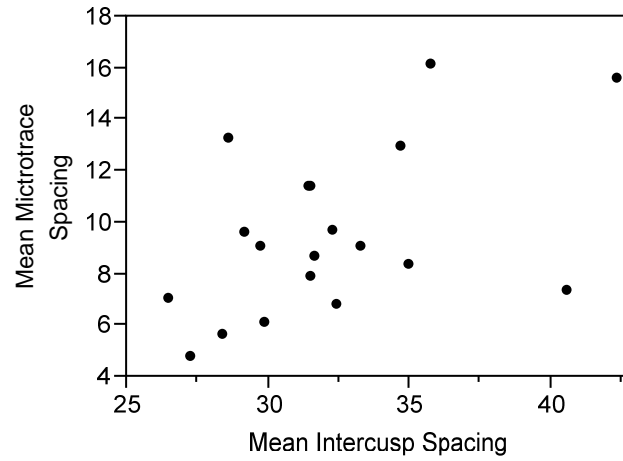
Figure 4. Correlation between mean microtrace and intercusp spacing. Mean spacing between microtraces is significantly correlated with the mean radular intercusp spacing of the individual responsible for drilling (Pearson's _r_=0.50, _p_=0.03).

<div align="center">TABLES AND TABLE CAPTIONS</div>

Table 1. Mean microtrace spacing and intercusp spacing of the dentition for the corresponding drilling gastropod. Number of measurements is indicated by n. The standard deviation (SD) of microtrace spacing is high, as would be expected based on drilling behavior (positioning of the radula relative to the substrate and multiple passes). Note that each radular tooth has 3 cups, so a single tooth will have two measurements. Shell height of the predator (Height) is a proxy for size.

Nucella	Mean Microtrace Spacing (μm)	n	SD	Mean Intercusp Spacing (μm)	n	SD	Height (mm)
4	16.1	15	4.9	35.8	20	31.0	35.6
6	6.8	22	4.6	32.4	18	21.5	36.9
17	5.7	15	1.1	28.4	38	62.5	31.3
20	7.0	15	1.7	26.5	23	20.8	33.9
27	9.7	34	3.4	32.3	30	24.3	35.6
37	7.4	36	2.7	40.6	58	15.6	39.4
40	11.4	16	4.5	31.4	15	23.1	39.7
44	9.6	32	2.4	29.2	93	12.1	36.6
49	15.6	6	2.0	42.3	26	18.6	36.0
51	8.7	43	1.9	31.6	77	27.0	32.8
52	8.3	30	2.5	35.0	60	15.6	33.8
57	9.1	22	3.8	29.7	76	11.0	27.1
60	6.1	10	1.1	29.9	41	51.6	33.0
65	4.7	7	1.0	27.3	32	5.3	25.9
73	9.1	21	5.8	33.3	92	54.0	39.3
80	13.3	28	6.7	28.6	116	15.0	51.9
82	11.4	22	3.1	31.5	42	29.3	28.9
82.2	7.9	18	4.0	31.5	42	29.3	-
101	13.0	22	5.6	34.7	62	15.6	-

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APPENDIX D

MICROTRACE AND RADULA WIDTHS

Nucella No.	Nucella Height (mm)	Intercusp Spacing (µm)	Nucella No.	Nucella Height (mm)	Microtrace Spacing (µm)
4	35.62	30.78	4	35.62	9.94
4	35.62	32.02	4	35.62	10.20
4	35.62	33.26	4	35.62	10.47
4	35.62	29.10	4	35.62	10.72
4	35.62	29.26	4	35.62	13.03
4	35.62	33.44	4	35.62	13.29
4	35.62	31.73	4	35.62	14.96
4	35.62	27.55	4	35.62	15.79
4	35.62	29.88	4	35.62	16.74
4	35.62	29.72	4	35.62	17.01
4	35.62	38.71	4	35.62	19.78
4	35.62	40.06	4	35.62	20.44
4	35.62	40.53	4	35.62	22.12
4	35.62	41.64	4	35.62	22.48
4	35.62	40.87	4	35.62	24.62
4	35.62	38.24	6	36.94	2.28
4	35.62	44.43	6	36.94	2.34
4	35.62	43.50	6	36.94	2.43
4	35.62	41.18	6	36.94	2.65
4	35.62	39.78	6	36.94	2.84
6	36.94	27.34	6	36.94	2.84
6	36.94	25.55	6	36.94	3.10
6	36.94	25.48	6	36.94	3.30
6	36.94	25.96	6	36.94	3.40
6	36.94	30.33	6	36.94	3.46
6	36.94	30.63	6	36.94	4.10
6	36.94	31.56	6	36.94	4.18
6	36.94	33.13	6	36.94	4.22
6	36.94	28.95	6	36.94	10.44
6	36.94	30.50	6	36.94	10.44
6	36.94	36.51	6	36.94	11.39
6	36.94	39.02	6	36.94	11.75
6	36.94	37.14	6	36.94	12.16
6	36.94	38.72	6	36.94	12.24
6	36.94	33.61	6	36.94	13.42
6	36.94	34.67	6	36.94	13.59
6	36.94	36.54	6	36.94	13.65
6	36.94	38.10	17	31.3	3.53
17	31.3	15.45	17	31.3	3.74
17	31.3	16.22	17	31.3	5.16

17	31.3	30.31	17	31.3	5.18
17	31.3	28.82	17	31.3	5.29
17	31.3	25.32	17	31.3	5.69
17	31.3	30.09	17	31.3	5.82
17	31.3	24.65	17	31.3	5.85
17	31.3	29.28	17	31.3	5.90
17	31.3	35.35	17	31.3	5.93
17	31.3	37.11	17	31.3	5.93
17	31.3	33.64	17	31.3	5.99
17	31.3	30.14	17	31.3	6.07
17	31.3	29.10	17	31.3	6.45
17	31.3	31.73	17	31.3	8.26
17	31.3	30.57	20	33.93	4.84
17	31.3	29.30	20	33.93	5.55
17	31.3	26.14	20	33.93	6.00
17	31.3	16.57	20	33.93	6.00
17	31.3	12.52	20	33.93	6.00
17	31.3	16.16	20	33.93	6.23
17	31.3	18.54	20	33.93	6.31
17	31.3	19.63	20	33.93	6.31
17	31.3	13.85	20	33.93	6.39
17	31.3	18.22	20	33.93	6.88
17	31.3	23.27	20	33.93	7.16
17	31.3	27.54	20	33.93	8.08
17	31.3	32.11	20	33.93	8.73
17	31.3	35.40	20	33.93	9.21
17	31.3	37.62	20	33.93	11.26
17	31.3	34.54	27	35.55	4.97
17	31.3	34.65	27	35.55	5.14
17	31.3	35.50	27	35.55	5.35
17	31.3	42.11	27	35.55	5.61
17	31.3	33.25	27	35.55	5.77
17	31.3	36.33	27	35.55	6.73
17	31.3	37.45	27	35.55	6.86
17	31.3	32.10	27	35.55	7.29
17	31.3	37.67	27	35.55	7.39
20	33.93	16.90	27	35.55	7.41
20	33.93	23.42	27	35.55	7.51
20	33.93	25.37	27	35.55	7.57
20	33.93	30.25	27	35.55	7.69
20	33.93	29.05	27	35.55	8.31
20	33.93	30.25	27	35.55	8.31
20	33.93	29.32	27	35.55	8.58
20	33.93	28.36	27	35.55	8.59
20	33.93	25.46	27	35.55	9.47
20	33.93	26.24	27	35.55	9.69
20	33.93	20.78	27	35.55	9.72
20	33.93	24.48	27	35.55	9.85
20	33.93	22.31	27	35.55	9.94

20	33.93	27.15	27	35.55	10.02
20	33.93	22.35	27	35.55	10.29
20	33.93	26.41	27	35.55	11.49
20	33.93	21.42	27	35.55	11.93
20	33.93	19.99	27	35.55	12.33
20	33.93	30.88	27	35.55	12.62
20	33.93	34.04	27	35.55	14.05
20	33.93	28.59	27	35.55	14.38
20	33.93	34.89	27	35.55	14.96
20	33.93	30.51	27	35.55	15.00
27	35.55	32.22	27	35.55	17.20
27	35.55	28.51	27	35.55	17.54
27	35.55	29.29	37	39.38	3.60
27	35.55	25.41	37	39.38	3.64
27	35.55	22.72	37	39.38	3.94
27	35.55	23.79	37	39.38	4.02
27	35.55	24.77	37	39.38	4.58
27	35.55	28.64	37	39.38	4.77
27	35.55	30.28	37	39.38	4.85
27	35.55	31.05	37	39.38	4.96
27	35.55	34.27	37	39.38	5.33
27	35.55	36.35	37	39.38	5.53
27	35.55	36.14	37	39.38	5.82
27	35.55	37.08	37	39.38	6.10
27	35.55	40.08	37	39.38	6.20
27	35.55	34.83	37	39.38	6.29
27	35.55	37.62	37	39.38	6.67
27	35.55	36.63	37	39.38	6.78
27	35.55	40.31	37	39.38	6.86
27	35.55	35.85	37	39.38	6.86
27	35.55	38.04	37	39.38	6.88
27	35.55	34.89	37	39.38	6.90
27	35.55	36.96	37	39.38	6.90
27	35.55	36.23	37	39.38	7.09
27	35.55	33.64	37	39.38	7.26
27	35.55	29.03	37	39.38	7.31
27	35.55	28.63	37	39.38	7.69
27	35.55	27.94	37	39.38	8.48
27	35.55	29.70	37	39.38	9.17
27	35.55	28.30	37	39.38	9.44
37	39.38	46.74	37	39.38	9.51
37	39.38	45.63	37	39.38	9.51
37	39.38	46.37	37	39.38	10.09
37	39.38	41.45	37	39.38	10.54
37	39.38	44.22	37	39.38	11.43
37	39.38	44.22	37	39.38	12.15
37	39.38	39.20	37	39.38	12.73
37	39.38	39.50	37	39.38	15.13
37	39.38	38.10	40	39.67	5.61

37	39.38	36.13	40	39.67	6.18
37	39.38	31.59	40	39.67	6.25
37	39.38	34.60	40	39.67	7.90
37	39.38	36.89	40	39.67	8.03
37	39.38	38.20	40	39.67	8.09
37	39.38	37.07	40	39.67	8.42
37	39.38	39.28	40	39.67	10.31
37	39.38	38.10	40	39.67	10.53
37	39.38	37.29	40	39.67	12.36
37	39.38	37.92	40	39.67	13.74
37	39.38	37.03	40	39.67	14.68
37	39.38	41.48	40	39.67	16.34
37	39.38	44.02	40	39.67	16.84
37	39.38	43.99	40	39.67	17.60
37	39.38	42.75	40	39.67	19.45
37	39.38	42.94	44	39.67	6.10
37	39.38	44.02	44	39.67	6.18
37	39.38	43.72	44	39.67	6.23
37	39.38	44.43	44	39.67	6.38
37	39.38	42.75	44	39.67	7.08
37	39.38	38.95	44	39.67	7.31
37	39.38	37.78	44	39.67	7.49
37	39.38	37.22	44	39.67	7.85
37	39.38	34.74	44	39.67	8.17
37	39.38	39.84	44	39.67	8.25
37	39.38	37.80	44	39.67	8.34
37	39.38	39.58	44	39.67	8.37
37	39.38	41.52	44	39.67	8.53
37	39.38	42.55	44	39.67	9.22
37	39.38	41.42	44	39.67	9.64
37	39.38	46.27	44	39.67	9.73
37	39.38	45.31	44	39.67	9.78
37	39.38	44.95	44	39.67	9.78
37	39.38	46.85	44	39.67	9.86
37	39.38	45.47	44	39.67	9.91
37	39.38	46.37	44	39.67	10.11
37	39.38	36.24	44	39.67	10.11
37	39.38	43.86	44	39.67	10.84
37	39.38	39.64	44	39.67	10.94
37	39.38	44.80	44	39.67	10.94
37	39.38	33.43	44	39.67	11.05
37	39.38	31.51	44	39.67	11.09
37	39.38	33.93	44	39.67	11.31
37	39.38	38.61	44	39.67	13.43
37	39.38	40.54	44	39.67	13.53
37	39.38	41.49	44	39.67	14.22
37	39.38	40.54	44	39.67	15.53
37	39.38	41.04	49	35.99	12.08
37	39.38	40.69	49	35.99	14.84

40	39.67	30.46	49	35.99	15.29
40	39.67	28.80	49	35.99	16.19
40	39.67	21.62	49	35.99	17.11
40	39.67	26.85	49	35.99	17.81
40	39.67	28.93	51	32.75	5.60
40	39.67	34.06	51	32.75	5.69
40	39.67	37.19	51	32.75	5.79
40	39.67	35.68	51	32.75	6.34
40	39.67	34.30	51	32.75	6.57
40	39.67	26.33	51	32.75	6.79
40	39.67	37.74	51	32.75	6.79
40	39.67	36.25	51	32.75	6.83
40	39.67	26.73	51	32.75	7.05
40	39.67	35.26	51	32.75	7.22
40	39.67	31.35	51	32.75	7.22
44	39.67	27.59	51	32.75	7.24
44	39.67	29.69	51	32.75	7.45
44	39.67	29.92	51	32.75	7.66
44	39.67	31.58	51	32.75	7.66
44	39.67	33.86	51	32.75	7.80
44	39.67	31.66	51	32.75	8.02
44	39.67	33.67	51	32.75	8.03
44	39.67	33.50	51	32.75	8.46
44	39.67	34.40	51	32.75	8.46
44	39.67	34.42	51	32.75	8.46
44	39.67	31.79	51	32.75	8.47
44	39.67	31.97	51	32.75	8.63
44	39.67	34.48	51	32.75	8.78
44	39.67	28.08	51	32.75	8.81
44	39.67	31.51	51	32.75	8.89
44	39.67	27.16	51	32.75	9.15
44	39.67	23.61	51	32.75	9.24
44	39.67	26.00	51	32.75	9.30
44	39.67	28.39	51	32.75	9.30
44	39.67	27.66	51	32.75	9.31
44	39.67	30.40	51	32.75	9.76
44	39.67	29.30	51	32.75	9.87
44	39.67	33.15	51	32.75	10.17
44	39.67	28.72	51	32.75	10.32
44	39.67	30.55	51	32.75	10.46
44	39.67	29.82	51	32.75	10.60
44	39.67	30.18	51	32.75	10.60
44	39.67	29.85	51	32.75	10.70
44	39.67	30.94	51	32.75	10.83
44	39.67	32.97	51	32.75	11.41
44	39.67	30.39	51	32.75	11.42
44	39.67	29.10	51	32.75	15.05
44	39.67	28.01	52	33.82	4.24
44	39.67	25.52	52	33.82	4.69

44	39.67	23.49	52	33.82	4.86
44	39.67	26.88	52	33.82	4.99
44	39.67	31.60	52	33.82	5.26
44	39.67	34.25	52	33.82	5.84
44	39.67	35.15	52	33.82	6.24
44	39.67	36.25	52	33.82	6.49
44	39.67	36.15	52	33.82	6.92
44	39.67	34.64	52	33.82	7.07
44	39.67	33.87	52	33.82	7.07
44	39.67	30.38	52	33.82	7.12
44	39.67	30.89	52	33.82	7.18
44	39.67	29.66	52	33.82	7.53
44	39.67	27.47	52	33.82	7.73
44	39.67	26.43	52	33.82	8.65
44	39.67	24.41	52	33.82	8.89
44	39.67	24.24	52	33.82	9.15
44	39.67	26.91	52	33.82	9.16
44	39.67	24.92	52	33.82	9.19
44	39.67	25.26	52	33.82	9.30
44	39.67	24.92	52	33.82	9.50
44	39.67	25.01	52	33.82	9.79
44	39.67	26.87	52	33.82	10.53
44	39.67	24.66	52	33.82	10.60
44	39.67	26.03	52	33.82	11.16
44	39.67	32.77	52	33.82	11.26
44	39.67	30.19	52	33.82	12.81
44	39.67	29.96	52	33.82	13.06
44	39.67	32.43	52	33.82	13.33
44	39.67	33.91	57	27.14	4.59
44	39.67	31.75	57	27.14	5.25
44	39.67	32.42	57	27.14	5.30
44	39.67	30.93	57	27.14	5.51
44	39.67	30.43	57	27.14	5.78
44	39.67	28.75	57	27.14	6.17
44	39.67	26.36	57	27.14	6.29
44	39.67	26.90	57	27.14	6.73
44	39.67	25.08	57	27.14	6.78
44	39.67	28.19	57	27.14	7.49
44	39.67	25.26	57	27.14	7.80
44	39.67	28.18	57	27.14	8.00
44	39.67	28.91	57	27.14	8.65
44	39.67	28.17	57	27.14	9.68
44	39.67	28.02	57	27.14	10.63
44	39.67	24.00	57	27.14	10.64
44	39.67	25.03	57	27.14	10.81
44	39.67	22.64	57	27.14	12.63
44	39.67	25.34	57	27.14	12.74
44	39.67	32.70	57	27.14	13.43
44	39.67	31.41	57	27.14	16.11

44	39.67	26.78	57	27.14	18.56
44	39.67	23.22	60	32.96	4.21
44	39.67	21.63	60	32.96	5.46
44	39.67	22.72	60	32.96	5.68
44	39.67	26.37	60	32.96	5.68
44	39.67	27.79	60	32.96	5.86
44	39.67	30.20	60	32.96	6.15
44	39.67	31.48	60	32.96	6.29
44	39.67	32.01	60	32.96	6.33
44	39.67	31.12	60	32.96	7.54
49	35.99	39.23	60	32.96	7.99
49	35.99	36.28	65	25.9	3.79
49	35.99	38.94	65	25.9	3.92
49	35.99	35.10	65	25.9	4.30
49	35.99	38.35	65	25.9	4.46
49	35.99	38.05	65	25.9	4.62
49	35.99	38.36	65	25.9	5.32
49	35.99	38.35	65	25.9	6.81
49	35.99	40.71	73	39.3	2.83
49	35.99	39.09	73	39.3	4.52
49	35.99	38.72	73	39.3	4.93
49	35.99	41.31	73	39.3	5.17
49	35.99	38.72	73	39.3	5.17
49	35.99	46.61	73	39.3	5.57
49	35.99	47.49	73	39.3	5.74
49	35.99	45.13	73	39.3	6.00
49	35.99	46.03	73	39.3	6.38
49	35.99	50.15	73	39.3	6.46
49	35.99	50.44	73	39.3	7.70
49	35.99	46.61	73	39.3	7.98
49	35.99	46.61	73	39.3	8.11
49	35.99	43.36	73	39.3	8.31
49	35.99	43.88	73	39.3	9.47
49	35.99	43.51	73	39.3	9.57
49	35.99	45.72	73	39.3	10.77
49	35.99	44.25	73	39.3	13.75
51	32.75	31.39	73	39.3	15.47
51	32.75	32.64	73	39.3	18.64
51	32.75	32.26	73	39.3	27.78
51	32.75	36.43	80	51.89	3.98
51	32.75	35.11	80	51.89	4.11
51	32.75	34.73	80	51.89	4.34
51	32.75	32.83	80	51.89	4.66
51	32.75	30.55	80	51.89	4.71
51	32.75	32.83	80	51.89	5.31
51	32.75	34.16	80	51.89	5.51
51	32.75	36.24	80	51.89	6.25
51	32.75	40.43	80	51.89	10.54
51	32.75	37.01	80	51.89	10.67

51	32.75	38.21	80	51.89	12.44
51	32.75	42.14	80	51.89	12.56
51	32.75	38.35	80	51.89	12.56
51	32.75	37.21	80	51.89	12.91
51	32.75	37.26	80	51.89	13.05
51	32.75	41.19	80	51.89	13.77
51	32.75	36.82	80	51.89	14.53
51	32.75	33.97	80	51.89	14.94
51	32.75	44.08	80	51.89	15.08
51	32.75	36.97	80	51.89	17.15
51	32.75	34.64	80	51.89	17.30
51	32.75	37.68	80	51.89	18.41
51	32.75	31.68	80	51.89	21.11
51	32.75	31.64	80	51.89	21.11
51	32.75	31.09	80	51.89	21.11
51	32.75	29.34	80	51.89	24.05
51	32.75	28.09	80	51.89	24.24
51	32.75	29.64	80	51.89	25.19
51	32.75	31.57	82	28.89	6.44
51	32.75	24.78	82	28.89	7.57
51	32.75	29.65	82	28.89	8.45
51	32.75	22.14	82	28.89	8.47
51	32.75	22.79	82	28.89	8.92
51	32.75	28.06	82	28.89	9.30
51	32.75	32.33	82	28.89	9.41
51	32.75	32.24	82	28.89	9.70
51	32.75	30.11	82	28.89	10.39
51	32.75	33.59	82	28.89	10.48
51	32.75	31.15	82	28.89	10.96
51	32.75	33.97	82	28.89	11.17
51	32.75	31.51	82	28.89	11.74
51	32.75	31.50	82	28.89	11.95
51	32.75	33.02	82	28.89	12.31
51	32.75	33.02	82	28.89	12.59
51	32.75	34.35	82	28.89	12.68
51	32.75	33.62	82	28.89	12.78
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CHAPTER 5

CONCLUSIONS

In summary, the findings of each study are outlined here: In feeding experiments whole, live brachiopods were willingly consumed by three common marine invertebrate predators (crustaceans, echinoderms, and gastropods) with no visible adverse effects. Systematic field surveys examining the frequency of predation traces (repair scars) on the local brachiopod population signify that predation pressure in the brachiopod community may be noteworthy. In addition, the fossil record yields a plethora of quantitative data documenting an extensive history of predation on brachiopods. Therefore, predation should still be considered a potentially important factor in brachiopod ecology and evolution, and although not preferred prey, we found no indication that rhynchonelliform brachiopods are toxic. Localities with high predation rates may, therefore, represent prey-rank abundance patterns. For example, predator preference for other prey (such as bivalves) would result in low trace frequencies in mixed assemblages where preferred prey types are abundant, and high trace frequencies in assemblages dominated by brachiopods. Additional studies targeting mixed brachiopod bivalve assemblages with variable abundances of preferred prey types are needed to assess this hypothesis.

Feeding trials using limpets indicate that low-spires and smooth shells may be antipredatory adaptions to durophagous predation, and crab attack behaviors suggest that large size and greater shell edge thickness may also be important in increasing survivorship. As species possessing high-spires and ridges typically occur high in the intertidal where predation risk due to crabs is relatively low, these morphologies are likely adaptions to physical factors such as thermal stress. As edge thickness may be increase survivorship, additional study is needed to determine whether shell ornament serves to strengthen the limpet shell as it does in spirally coiled gastropods. Furthermore, studies documenting size refugia (a size at which the prey is too large to be taken) in limpets would augment our understanding of the importance of predation by adult cancrid crabs.

Replication of microtraces using wax substrates confirmed that radular teeth of predatory gastropods are capable of generating parallel grooves of varying numbers and depths, on soft substrates. Overall, microtraces provide a reasonable approximation of the size of the radular dentition (i.e., intercusp spacing), and replicated traces closely resemble microtraces observed within drill holes. Artificially replicated drill holes demonstrate that shell crystalline microstructure observed in cross section is typically uniform, and no microtraces were found in replicated drill holes. These data confirm that traces observed on the walls of complete drill holes are indeed the result of radular rasping, and not simply crystalline microarchitecture of the shell. The feasibility of extracting ecological information from drilling predation microtraces was also determined by measuring microtrace spacing and intercusp spacing of radulae dentition of the predators that created the drill hole. Microtrace spacing measured from electron micrographs correlates well with intercusp spacing, and radular rasp marks may be used to extrapolate intercusp spacing. Drilling microtraces could, therefore, provide valuable insight into drill hole origins in contentious, or degraded specimens. While rasp marks may be used to estimate the size of the radula, radula size does not appear to increase in concert with gastropod size for adult *Nucella lamellosa*. Radular rasp marks, therefore, do not serve as a proxy for predator size. Examination of rasp marks produced by several other radular configurations, and including predatory gastropods from other groups (e.g., naticids), could prove a fruitful avenue for future investigations. If radular rasp marks can be used to differentiate between predator groups on the basis of radular morphology, drilling predation microtraces could provide invaluable insights in to the identity of predators in the fossil record.

Research that focuses on organismal interactions, and techniques to examine these interactions, is continually uncovering novel information on the history of life on Earth. The development of a clearer understanding of complex community interactions such as predation on evolutionary timescales requires the synthesis of micro- and macro- scale analyses. Therefore, we must continue to explore proxies for predation intensity such as predation traces or antipredatory morphologies. These types of paleoecological data are also of interest to both paleontologists and biologists, as the need to understand the role of predation in the regulation of biodiversity and evolution is becoming increasingly important in conservation and ecosystem management.