PREDATION IN MOLLUSCS: A MULTI-TAXON APPROACH USING NEONTOLOGICAL AND PALEONTOLOGICAL DATA

by

Devapriya Chattopadhyay

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Geology)
in The University of Michigan
2009

Doctoral Committee:

Professor Tomasz K. Baumiller, Chair
Professor Daniel C. Fisher
Professor Kyger C. Lohmann
Assistant Professor Thomas F. Duda Jr.
Assistant Professor Jeffrey A. Wilson
Research Scientist Janice L. Pappas

ACKNOWLEDGEMENTS

I want to extend my sincere gratitude to my academic adviser Prof. Tomasz K. Baumiller who introduced me to the modern trends in Paleontology. I wish to thank Prof. Michal Kowalewski of Virginia Polytechnic Institute and State University and Prof. Lindsey Leighton of University of Alberta who helped me to carry out the neontological experiments. Special thanks to Dr. Daniel J. Miller and G. Alex Janevski for numerous valuable discussions that significantly improved my dissertation. UROP student Sarah Groat helped me in collecting data from the museum specimens. I would like to thank my collaborator Ms. Michelle Casey (Yale University) for her part in our joint study that I included as an appendix in this dissertation. I am indebted to Dr. John Huntley for sharing his data on Phanerozoic predation intensity (Chapter VI). I wish to thank Ms. Anne Hudon for her unrelenting help with all official procedures that could be quite challenging for an international student. My sincere thanks to all the members of Museum of Paleontology who provided useful criticism that improved my work. My husband, Anirban Dutta stood by me in good time and in not so good times. I am grateful to my family members who supported me to reach my goal. This work was supported by grants from the Department of Geological Sciences of University of Michigan, Rackham Graduate School of University of Michigan, Conchologists of America, Friday Harbor Laboratory of University of Washington and Geological Society of America.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

This work is a collection of five independent manuscripts that are united under the general theme of ecological and evolutionary consequences of predation among Cenozoic molluscs. In modern marine environment, predation is a significant agent of natural selection. However, evidence of predation in fossils is generally rare, primarily because most predators destroy the prey or leave no traces on any preservable hard parts of the victim. Drilling predation of shelled marine invertebrates by muricid and naticid gastropods represents one of the very rare instances that allow biotic interactions to be evaluated quantitatively in the Recent and in the geologic record. Not surprisingly, drill holes have been used as an important source of information on the nature of biotic interactions and to explore the ecological and evolutionary roles of such interactions (Vermeij, 1987; Kelley and Hansen, 1993). Quantitative measures employed to study predation include the frequency of drill holes used to estimate predation intensity (Taylor, 1970; Stanton and Nelson, 1980; Vermeij *et al.*, 1980; Vermeij and Dudley, 1982; Kabat and Kohn, 1986), frequencies of incomplete drill holes used as a measure of failed predation events (but see Kowalewski, 2004), and thus prey-effectiveness (Kelley and Hansen, 2001), position of drill holes and distribution of sizes of prey used to evaluate predatory strategies, and taxonomic distribution of drill holes used to explore selectivity. Drilling frequencies have also been used to test hypotheses about prey-selectivity (Ausich and Gurrola, 1979; Vermeij and Dudley, 1982; Hoffman and Martinell, 1984; Colbath, 1985; Tull and Bohning-Gaese, 1993; Leighton, 2003), predator behavior (Berg and Nishenko, 1975; Zlotnik, 2001; Deline *et al.*, 2003) and to explore broad scale temporal patterns in predation intensity (Vermeij, 1987; Kelley & Hansen, 1993; Kowalewski *et al.*, 1998; Huntley & Kowalewski, 2007).

These studies generally rely on the assumption that drilling predation data have not undergone any taphonomic alteration that could generate a bias. In Chapter II, I investigated one potential taphonomic bias that relates to the hydrodynamic properties of shells: presence of drill holes and/or drill hole position may influence how shells behave when subjected to moving fluids. In a flow tank study with bivalves, I found that the threshold current velocity for the entrainment of undrilled convex-up shells is significantly lower than for centrally drilled shells. The position of the drill hole on a shell also affects its hydrodynamic properties: umbonally drilled shells always have lower entrainment velocity compared to centrally drilled shells. I also developed models to predict the patterns that could be generated by this bias in a hydrodynamically affected assemblage.

In Chapter III and IV, I investigated various aspects of predator-prey dynamics. In Chapter III, I report the results from a simple two taxon system (drilling predator and a prey) that investigated the details of their feeding behavior. For cost-benefit analyses, accurate measurement of penetration rate and consumption rate are essential. I determined the penetration rate and consumption rate of the muricid gastropod *Nucella lamellosa* preying upon the mussel, *Mytilus trossulus*. I also developed a new metric, “excavation rate”, which is better suited for quantifying the amount of work done by the driller since it is defined as the amount of shell material excavated per unit of time.

In Chapter IV, using the drilling muricid, *Nucella lamellosa,* and its prey, the mussel *Mytilus trossulus*, I investigated the behavior of a drilling predator in the presence of a secondary, durophagous predator (crab). I noted a significant difference in frequencies of complete and incomplete drill holes when the crab was present.

The neontological experiments described in Chapter IV demonstrated that in the presence of a secondary predator (crab), the incomplete drilling frequency increases indicating increasing abandonment of the prey, and drilling frequency decreases, implying a decrease in successful attacks. In Chapter V, I tested whether the effect of secondary predators on drilling frequencies can be detected in the fossil record. Using fossil mollusks from six Plio-Pleistocene localities, I evaluated the relationship between that repair scar frequencies, a proxy for activity of durophagous predators, and frequencies of complete and incomplete drill hole.

In Chapter VI, I extended my previous findings to a broader temporal and geographic scale. Using a large global data set on Cenozoic drilling and durophagous predation intensity, I evaluated whether the fluctuation in drilling predation intensity could be explained by the changes in durophagous predation intensity. I also tested if the changing diversity of predatory groups is reflected in the predation intensity.

Finally, I investigated the effectiveness of certain behavioral traits of the prey against drilling predation. Previous studies have shown that mussels use clumping behavior against durophagous predation, but its role against drilling predation had not been explored. With M. Casey (Department of Geological Sciences, Yale University), we explored the effect of clumping on predator success (drill-hole frequency) and prey handling (drill-hole position) using the mussel, *Mytilus trossulus,* as prey and the gastropod, *Nucella lamellosa,* as drilling predator (Appendix). We observed a significant decrease in the drilling frequency within the group containing clumped mussels, confirming that clumping acts as a successful anti-predatory strategy against drilling predators.

CHAPTER 2

HYDRODYNAMIC EFFECTS OF DRILL HOLES ON POST-MORTEM TRANSPORTATION OF BIVALVE SHELLS

Introduction

The traces of predation made by drilling gastropods represent an important source of information on the nature of biotic interactions and have often been used to explore the ecological and evolutionary roles of such interactions. Because drilled shells are commonly preserved in the fossil record, drill holes have been used as an important source of information on the nature of biotic interactions (Hoffman *et al.*, 1974; Hoffman, 1976; Taylor *et al.*, 1983; Vermeij, 1983, 1987; Kelley, 1989, 1991; Anderson, 1992; see Kelley *et al.*, 2003 for review). For example, the frequency of drill holes has been used to estimate predation intensity (Taylor, 1970; Stanton and Nelson, 1980; Vermeij *et al.*, 1980; Vermeij and Dudley, 1982; Kabat and Kohn, 1986) while the consistency of drill-hole placement on prey shells (drill-hole stereotypy) and the drill-hole's correspondence to internal anatomy have been used to infer important information about predator behavior in the fossil record (Kelley and Hansen, 2003 and references therein). The tacit assumption of these studies, however, is that patterns of drilling are not altered by taphonomic processes. Although some workers have explored the potential for taphonomic bias due to differences in mechanical strength (Roy *et al.* 1994, Kaplan and Baumiller, 2000; Zuschin and Stanton, 2001), other potential biases remain largely untested. In this study we explore differences in hydrodynamic behavior between drilled and undrilled bivalve shells and examine the potential consequences for ecological and paleoecological analyses.

Previous studies:

Workers have cautioned that a number of effects can mask the true boring intensity and lead to misinterpretation of an assemblage's paleoecology (De Cauwer, 1985; Velbel and Brandt, 1989; Harper *et al.*, 1998). These effects include the differential resistance of valves to taphonomic forces before or after burial, the destruction of valves by non-drilling durophages and the sorting of valves by currents or other agents. Roy *et al.* (1994) found a significant difference in strength between drilled and undrilled *Mulinia* valves; the bored ones are weaker under point load compression. Nonetheless, this bias does not exist in a high energy environment (Hagstrom, 1996) or sediment compaction (Kaplan and Baumiller, 2000; Zuchin and Stanton, 2001). If the two valves differ in shape and/or thickness (a very common phenomena for brachiopods shells) that might lead to an unequal preservation probability for different valves (Velbel and Brandt, 1989). This preferential removal of a particular valve might alter the original drilling frequency (Kaplan and Baumiller, 2000). Similar bias could also result by destruction of undrilled valves by non-drilling durophagous predators (Vermeij *et al.*, 1989).

The hydrodynamic properties of a shell depend on a number of factors. Several studies have examined current competencies required to reorient brachiopod shells, as well as, the subsequent alignment of the shell after transport (Menard and Boucot, 1951; Johnson, 1958; Nagle, 1967; Alexander, 1975, 1984, 1986; LaBarbera, 1977; Savarese, 1994; Quaresma *et al.*, 2007). Menard and Boucot (1951) observed that shape, size, effective density and ornamentation influence the competent velocity of a brachiopod shell. Wave and current action continually remove shells that have lower competent velocity and redeposit them at the dictate of local currents. This nature of preferential removal and redeposition could result in a substantial difference between life and death assemblage (Boucot, 1953). Boucot *et al.* (1958) described a statistical method that helps to discriminate life and death assemblages of brachiopod and bivalve shells. However, Messina and LaBarbera (2004) found no significant difference in entrainment velocities of brachiopod shells of different size and shape. Similar studies conducted on bivalve shells explored at the effect of shape, size, initial orientation and grain size of the associated sediments on entrainment velocity (Brenchley and Newall, 1970; Trewin and Welsh, 1972; Futterer, 1982; Allen, 1984; McKittrick, 1987; Frey and Dörjes, 1988;

Olivera and Wood, 1997). These differences could alter overall drilling frequency by preferential removal of a particular group of shells (size class, shape class, taxa).

The minor differences between right and left valve geometry of a bivalve shell could result in a completely different transportation pattern. A study on bivalve shells collected on Trinidad beach by P. Martin-Kaye documented that postmortem transportation could result in a different distribution of right and left valves. The two valves of the bivalve *Pitar dione* are exact mirror images of each other. Because of this asymmetry, they were not transported in the same manner by the waves (Martin-Kaye, P. 1951). Boucot *et al.* (1958) predicted that asymmetric mirror-image shells will tend to diverge dextrally and sinistrally from the direction of the current, and therefore result in a sorted assemblage. Similar phenomena have been reported in other studies (Lever, 1958; Konicker *et al.*, 1963; Nagle, 1964; Lever and Thijssen, 1968; Behrens and Watson, 1969; Frey and Henderson, 1987; Ellers, 1995). If the drilling predators tend to prefer drilling one valve over the other, this preferential loss of valve might alter the true drilling frequency.

However, a more direct effect on drilling frequency could be imagined if the hydrodynamics of a shell depends on the presence/absence of a hole. Lever *et al.* (1961), in a mark and recapture experiment, demonstrated that drilled and undrilled valves exhibit different hydrodynamic behavior; they found that umbonally drilled valves were carried higher onto the beach compared to the undrilled shells. In a similar study, Miller showed the difference in entrainment velocity between drilled and undrilled valves (Miller, 1991).

Conceptual model:

The two main forces that act on a shell in a fluid flow, resting on a plane bottom, are drag force F_D, acting parallel to the direction of the flow and lift force F_L, acting perpendicular to the flow (Fig. 2.1). Drag is generated from both shear stress on the shell surface and pressure difference between the areas of the shell surface oriented into and away from the flow. For a shell resting on a plane surface, flow velocity beneath the shell is zero and therefore, lift is dependent upon the velocity distribution over the top of the valve.

The gravity force, proportional to the mass, is independent of fluid action and is represented by the weight of the shell. When the body is submerged, it experiences a buoyancy force exerted by the fluid, equal to the weight of the displaced volume of the fluid. The buoyancy force and the weight act through the center of gravity in opposite directions. The net gravity force, F_{NG}, is therefore equal to the difference between the weight and buoyancy force.

The stability of the shell in a fluid flow is determined by the equilibrium of the forces acting on the body. Drag, lift and buoyancy can be considered destabilizing forces, whereas weight and friction can be regarded as a stabilizing force. Therefore, the stability of a shell in flow depends on the magnitude of drag and lift generated by the fluid, in relation to the friction and net gravity force.

A shell resting convex-up on the bottom, with umbo pointing upstream, will experience both lift and drag force. The convex shape of the shell would result in a crowding of streamlines on the top of the shell and, according to Bernoulli's principle, form a zone of relatively high velocity and low pressure (Vogel 1994). The region beneath the shell would experience no or very low velocity and relatively high pressure. The difference in pressure between the outside and inside of the shell will generate lift on the shell and if the force is sufficient, it could destabilize the shell (Fig. 2.2a).

For a drilled shell, however, the scenario is slightly different (Fig. 2.2b). The presence of a hole on the top of the shell permits the exchange of fluid between inside and outside of the shell. As a result the pressure difference (and, therefore, the resulting lift force) is less than it is for an undrilled shell. Hence, it should be more difficult to destabilize a drilled shell, and we predict that the entrainment velocity for an undrilled shell will be significantly lower than a comparable shell with a drill hole. However, if the hole is facing the fluid it could generate a vortex (Fig. 2.2c).

Shells are often subjected to different hydrodynamic conditions during postmortem transport; the entrainment velocity will, to some extent, determine their behavior in different hydrodynamic conditions. Thus, in situations where there is significant postmortem transport, sorting of drilled and undrilled shells of a species could occur as a result of differences in hydrodynamic behavior. Shells have complex shapes and predictive models of the behavior in flow are unavailable. A few studies have tried to evaluate these interactions of forces on a bivalve shell in a flowing fluid using complex modeling (Christensen, 1981; Dey, 2003). Olivera and Wood (1997) provided data showing that the distribution of pressures on bivalve shells in flow is very complex. Therefore, testing the difference in hydrodynamic behavior of drilled and undrilled shells is best approached empirically. In this study, we use drilled and undrilled valves of the Recent bivalve *Mulinia lateralis* to test the hypothesis that drill holes influence hydrodynamic behavior by reducing lift on the shell (thereby increasing entrainment velocity). We will also examine the effect of drill hole position and valve orientation.

Materials and methods

Bulk samples of disarticulated shells of *Mulinia lateralis* were collected on Seabrook Island, South Carolina. Samples contained drilled (centrally and umbonally) and undrilled valves (Fig. 2.3). Drill holes were all countersunk and typically naticid in character (Carriker and Yochelson, 1968). The size of the drill holes ranged from 0.4 to 4 mm. Shells that did not show any visible damage were used. For each valve, the maximum antero-posterior length was measured with digital calipers (±0.001 mm).

To measure the entrainment velocity in unidirectional flow, a recirculation flow tank driven by a propeller and variable speed motor was used (Vogel and LaBarbera, 1978) (Fig. 2.4). Initially the dial controlling the motor of the flow tank was calibrated by timing the movement of a drop of fluorocene dye in the flow over a known distance with a stop watch (10 trials, ±0.2cm/s). Afterwards, velocity was measured directly from the dial.

Each valve was placed in still water on a Plexiglas plate in the flow tank chamber with the umbo facing upstream. We chose Plexiglas rather than sediment because the frictional forces that stabilize the shell will vary with substrate type (sediment grain size, sorting, cohesiveness, etc.) and are likely to change dynamically as sediment shifts during flow. The use of Plexiglas permits us to minimize variation in frictional forces and focus on the influence of the drill hole. Velocity was gradually increased until downstream motion was initiated. Initial entrainment velocity is here defined as the minimum velocity at which the shell begins moving downstream. Continuous entrainment velocity is the minimum velocity required to sustain continuous downstream motion of the valve. Both initial and continuous entrainment velocities were recorded. Measurements were also taken for two other shell orientations with respect to current direction: umbo pointing downstream and maximum length parallel to the flow direction. However, for these trials, only the initial velocity was measured because often the shells reoriented themselves after the initial movement. The most stable position of the shell is when its umbo is pointing upstream.

To obtain a qualitative understanding of the pressure distributions and flow patterns around shells, we also performed dye injection experiments using shells and transparent plastic models. Single valves with a central drill hole were glued to a plate of Plexiglas and filled with fluorocene dye using a hypodermic needle and a syringe. The Plexiglas plate was then placed on the floor of the flow-tank and pattern of the dye escape was carefully observed as velocity was increased. Similar experiments were performed using a transparent plastic hemisphere.

Results

The mass of the shell is strongly correlated with the length for both drilled and undrilled shells (Fig.2.5) and there is not a significant difference between drilled and undrilled shells of similar length. We did not find strong contrast between the different categories of the specimens (centrally and umbonally drilled, undrilled) when they were oriented with umbo pointing downstream and maximum length parallel to the flow direction. We observed a difference only when they were oriented with the umbo pointing upstream (all the results reported below are for this orientation). The velocity for continuous movement was always higher than that for the initial movement. So from now on we are going to refer to them collectively as entrainment velocity.

The undrilled specimens show a complex pattern of changing entrainment velocity with change in size. Velocity is fairly high for smaller size class (<10mm), then it decreases for intermediate sizes (10-15mm) and increases for larger sizes (>15mm). The velocities for the smaller and largest size classes are comparable. They range between 18-23 cm/sec (Fig.2.6).

Drilled shells show no change in entrainment velocity with changes in size. However, there is a pronounced difference in velocity that depends on the position of the drill hole on the shell. The centrally drilled shells have significantly higher velocity (mean velocity 22 cm/sec) than that of the undrilled ones (mean velocity 20cm/sec) ($p < 0.05$). The umbonally drilled shell has a much lower velocity (mean velocity 16 cm/sec) compared to the centrally drilled ones ($p < 0.05$) (Fig.2.7).

There is a sharp contrast in the way the dye escaped between the shells with different positions of drill hole. For a centrally drilled shell, the dye escaped very slowly. In contrast, it escaped at a faster rate for an umbonally drilled shell. The water went through the hole and created a vortex inside the shell. A similar pattern has been observed with transparent plastic hemisphere models.

Discussion

Comparison of drilled and undrilled shells:

The threshold current velocity for the entrainment of undrilled convex-up shells is significantly lower than that for the centrally drilled shells. This confirms our theoretical prediction about the effect of the hole on lift. Lift is caused by a pressure gradient between the inside and outside of the shell. Using Bernoulli's principle, a pressure gradient develops as current moves over the outside of the shell (high velocity, low pressure) while the water inside the shell remains stationary (low velocity, high pressure) (Fig.2.2a). In the presence of a hole, the pressure gradient may be dissipated as water percolates through the drill hole; as a result the pressure difference between the outer surface and the inner one is less for a centrally drilled than an undrilled shell (Fig.2.2b). In our dye experiment, we observed that the dye escapes the shell through the centrally located drill hole.

However this mechanism does not explain the observed velocity difference between centrally and umbonally drilled shells. The dye injection experiments show that the water enters the umbonally drilled shells through the drill hole and creates a vortex. In contrast it took a much longer time for the dye to completely escape the shell in the case of a centrally drilled shell. Here the mixing process is very slow indicating that water does not enter very rapidly to create turbulence unlike that of the umbonally drilled shell. The turbulence might cause the initial instability which would finally lead to entrainment of the umbonally drilled shells (Savory and Toy, 1986; Manhart, 1998) (Fig. 2.2c). This observation, however, is consistent with the findings of Lever *et al.* (1961). They also found the velocity of umbonally drilled shells to be lower than the undrilled shells. In a mark and recapture experiment with different genera of bivalves, they found a significant contrast in the abundance of umbonally drilled shells between the top and the base of a slope. They explain the phenomena as "hole effect" where the umbonally drilled ones are preferentially carried to the top of the slope since they need lower entrainment velocity.

Potential taphonomic bias in size:

The flow tank experiment demonstrated that there is a predictable relationship between size and entrainment velocity for undrilled shells; the entrainment velocity for the smaller and larger size classes is comparatively higher than it is for the intermediate size class. That pattern is expected since the smaller shells require a greater lift force because of their close proximity to the boundary layer; the bigger ones also need similar force because of their higher mass. A similar concept of differential entrainment has led to construction of a Hjülstrom diagram for sediments (Hjülstrom, 1939). However we did not find any such pattern for drilled shells. It is not entirely clear why we don't see the pattern. It might be possible that to see the pattern in drilled valves, we need to use much larger shells. In this size range, however, the presence of the hole is affecting the entrainment velocity much more compared to the mass difference.

In the simplest scenario, the effect of differential transport could be manifested in two ways, and therefore creating two different types of assemblages: (1) transported assemblage, composed of the shells transported from an original assemblage, and (2) lag assemblage, composed of the shells that were left behind during transportation. Although both depend on the nature of the fluid flow, the final configuration of these individual assemblages could be far from being identical. Although in the natural world almost always we would expect to get some combination of the two; just to keep things simple we will look at the patterns in those two discrete assemblages.

Based on our experimental results, we can expect different size frequency distributions in these two types of assemblages. At low flow velocities, we can expect to see a size sorting among undrilled shells since the entrainment velocity for the smaller and larger size class is comparatively higher than the intermediate size class. Transported assemblages will only have an intermediate size class transported at a lower velocity, whereas the lag assemblage will have a bimodal size class distribution due to the preferential removal of intermediate size classes by low velocity flow. This situation would only arise in very low energy environments (Fig. 2.8). In an environment where the average velocity is higher than the highest velocity needed to move the smallest and/or the heaviest shell, we might see a less pronounced bias since all shells will be transported.

In our experiment with drilled *Mulinia lateralis*, we did not find a strong correlation between size and velocity. This suggests that taphonomic losses due to hydrodynamic sorting should be similar for all the size classes for drilled shells. In other words, there is unlikely to be sorting of drilled *Mulinia* shells by size. If this bias is true for other bivalves, then observed differences in the abundance of a particular size class of drilled valves in a fossil assemblage is more likely to be due to size preference of the predator. However, the exact nature of sorting in different bivalves depends on a number of factors and is beyond the scope of this study.

Potential taphonomic bias in stereotypy:

The results of this study indicate that in different velocities the drilled shells will be sorted according to the position of the drill hole. Because the entrainment velocity for umbonally drilled shells is significantly lower than that of the centrally drilled shells, we can think of scenarios where this difference would lead to a differential distribution of drilled shells in transported compared to lag assemblages. With a low velocity fluid flow, we can expect to see a selective entrainment of umbonally drilled shells among the drilled ones. Transported assemblages will only have a highly skewed distribution of drilled shells with majority of umbonally drilled shells and as a result, the lag assemblage will have a higher proportion of centrally drilled individuals which would have been left behind by the low velocity flow (Figs. 2.8, 2.9). But this situation is likely to arise in low energy environments. In an environment where the average velocity is higher than the average velocity needed to move the centrally drilled shells, we might not see a very pronounced bias since everything will be transported. However, if the settling velocities are different for drilled and undrilled shells, then even in a high energy environment we might see the effect of hydrodynamic sorting.

Implication for an assemblage:

The frequency of drilled shells in the assemblage is commonly reported as a measure of intensity of drilling gastropod predation (see Kelley, 2001, for a review). Such data have been used to identify preferred prey taxa (Hoffman and Martinell, 1984) and changes in predator-prey interactions through time (Vermeij, 1983, 1987; Kelley, 1989, 1991). Long-term changes in drilling frequencies have been interpreted as reflecting the changing importance of the mode of predation in benthic marine communities (Vermeij, 1987, for a review). In our experiment, we observed that hydrodynamic differences could lead to preferential loss of particular classes (drilled or undrilled); this would result in a value of calculated predation intensity that is different from the original one.

Although the combined effect of time-averaging and hydrodynamic sorting could be quite complex, just to get a sense of how it could change an assemblage at a particular time, we designed a scheme to calculate predation intensities as a function of velocity using our data set. We selected a specific velocity and counted all the drilled and undrilled shells with entrainment velocities lower than that velocity, representing the transported assemblage. The remainder constitutes the lag assemblage. We then calculated the drilling frequency (following Vermeij, 1980). The results show that inferred drilling frequency (and therefore the predation intensity) changes with increasing velocity for both the transported and lag assemblages. The difference between actual predation intensity (velocity = 0 cm/sec) and calculated intensities can be substantial for both the transported assemblage (Fig. 2.10) and lag assemblage (Fig. 2.11).

Because shell transport varies as a function of size, shape, and mass, different taxa of bivalves within a given assemblage could suffer varying degrees of transportation. It is possible that high variances observed in the proportion of drilled individuals among species and localities (Vermeij, 1980; Anderson, 1992) may reflect differential transportation rather than (or in addition to) biotic signals. The extent of transportation bias for each taxon should be estimated individually before intraspecific comparisons of predation intensities are undertaken. The relationship between predation intensity and velocity might affect local fossil assemblages; however, it is very unlikely to be a significant problem for long-term global trends in drilling frequency (Vermeij, 1987), because on those time scales the changes in velocity should be more or less randomly distributed.

Efforts have been made to show the changing pattern of stereotypy through geologic time (Roopnarine and Willard, 2001; Dietl *et al.*, 2001, Dietl and Alexender, 2004). Earlier studies of drill hole site selectivity have assumed that such stereotypy has only biological implications. It has been related to the way predators manipulate a prey item (Ziegelmeier, 1954), size and shape of the prey (Ansell, 1960; Stump, 1975; Kitchell, 1986; Reyment, 1999; Roopnarine and Willard, 2001), ontogenetic growth (Vignali and Galleni, 1986; Calvet, 1992), and access to particular soft parts (Hughes and Dunkin, 1984; Arua and Haque, 1989; Leighton, 2001). It has also been used to show a trend in stereotypy through time (Dietl *et al,* 2001). The present study demonstrates how stereotypic pattern of drill hole position could be produced by the preferential sorting of shells with each type of drill hole.

To illustrate the effect of the bias, we calculated the number of centrally vs umbonally drilled valves as a function of velocity using our data set. We selected a specific velocity, counted all the centrally drilled and umbonally drilled shells with entrainment velocities lower than that; that would constitute our transported assemblage and the rest would constitute the lag assemblage. The results show that the ratio of centrally vs. umbonally drilled shells changes with increasing velocity for both transported and lag assemblage. As a result, the calculated ratio could be very different from the actual (ratio for velocity = 0 cm/sec) for both the transported assemblage (Fig. 2.12) and the lag assemblage (Fig. 2.13). Our experiments suggest that like the drilling frequency, stereotypic pattern could also be generated by hydrodynamic sorting of shells. However, it is quite unlikely (if not impossible) to get a long term trend by hydrodynamic sorting.

Assessment of biases

Our results demonstrate that the recognition of postmortem transportation is important in studies of drilling predation. Inferred drilling frequency and the pattern of drill hole position (therefore, inferred stereotypic behavior) could be greatly influenced by hydrodynamic sorting. We believe that careful examination of hydrodynamic behavior of samples should permit an assessment of information loss resulting from postmortem transportation. However, an important thing to consider before we even start to think about criteria for identifying hydrodynamics biases is that very rarely do we see assemblages affected by the same hydrodynamic conditions representing a single time horizon (e.g., event bed). More often than not, we find time averaged assemblages. So it is much more complicated to identify ways to rule out the possibility of hydrodynamic bias. But there are few comparatively clear indications of the presence of hydrodynamic sorting. So, although we can never entirely rule out the possibility of this bias, we could at least try to identify the assemblages which have clearly been altered by this bias. There are sedimentary features indicative of current (imbricated grains, preferentially aligned shells, ripple marks, etc. (Reineck and Singh, 1975)). If the assemblage is associated with these features, the shells were most likely to have experienced hydrodynamic forces. However, sometimes extensive bioturbation could obscure these patterns. Right-left valve ratio is another very important indicator of hydrodynamic history. Strongly unequal number of right and left valve in an assemblage indicates the work of hydrodynamic forces (Martin-Kaye, P. 1951; Boucot *et al.*, 1958; Lever, 1958; Konicker *et al.*, 1963).

A similar indicator is the value of calculated drilling frequency. Following Vermeij's method (1980) the drilling frequency for disarticulated valves is calculated by the formulae DF = (# Drilled shells X 2) / # Total shells. If there is no bias, we can get at the highest, 100% drilling frequency in an assemblage where every shell is drilled. But if the calculated drilling frequency is higher than 100%, that indicates that the original assemblage has been preferentially altered.

Observed size frequency distributions may provide useful clues to identify hydrodynamically altered assemblages. Our experiments show that the entrainment velocity is a function of size for undrilled specimens. We also observed that the intermediate size class has the lowest velocity of entrainment. So while a high velocity flow transports all size classes, a flow below a certain critical threshold will only transport the intermediate size class. As a result, the lag assemblage would have a strongly bimodal size distribution. But for each taxon, depending on their shape, mass, and ornamentation, this critical threshold velocity might be different. So in each taxon, if we see a strong bimodal size distribution in undrilled shells, the chances are high that the assemblage has been hydrodynamically altered. A supporting fact would be a contrast with drilled shells since the entrainment velocity does not seem to depend on the size for drilled shells. Similar principle could be used to identify yet another criterion. Since umbonally drilled shells have lower velocity, a low velocity flow will transport them. It would also transport the intermediate size class of the undrilled shells. Therefore in the transported assemblage, we will have a range of size of umbonally drilled shells, but a comparatively narrower size range of undrilled shells. In other words, undrilled size class would be a subset of the drilled size class. In biotic interaction, we generally find the opposite scenario, where a predator selects a particular size class. So the drilled size class is a subset of the undrilled size class. Such a pattern (opposite to biotic interaction pattern), if found, clearly indicates the fact that the assemblage has been subjected to hydrodynamic forces.

Finally, one trend that could rule out the effect of hydrodynamic bias, would be a systematic non-random signal in drilling frequency and/or stereotypy. In a spatial or temporal series, the time averaging of hydrodynamic biases could mask the original biotic signals, but time averaging alone is unlikely to generate a persistent temporal or spatial trend. So if the study of time averaged samples reveals a temporal trend, then most-likely it is indicating a true biotic signal, not a hydrodynamic artifact. We recommend, however, to exercise extreme caution when using specimens from single time units (event bed for instance) since the hydrodynamic sorting could greatly alter their assemblage in terms of drilling frequency and stereotypy.

Conclusion

Drill holes in the shells of invertebrates represent one of the most unambiguous signatures of predator-prey interactions and have been commonly used by neontologists and paleontologists to explore ecological and evolutionary questions. However there is comparatively smaller number of studies that looked at the potential taphonomic biases affecting the records of drilling predation. Here, we discussed one such taphonomic bias, namely hydrodynamic sorting. Using disarticulated specimens of *Mulinia lateralis* and a recirculation flow tank, we determined the entrainment velocities of both drilled and undrilled valves. The results of the flow tank experiment clearly demonstrate that there is a significant difference in entrainment velocity between drilled and undrilled shells: undrilled shells have a significantly lower entrainment velocity compared to centrally drilled shells. The size of the shell plays an important role in the movement of undrilled shells; both small and large shells are characterized by a higher entrainment velocity compared to the intermediate size class. The entrainment velocity is also affected by the position of the drill hole; umbonally drilled shells have significantly lower entrainment velocity compared to centrally drilled ones. However further work needs to be done on this factor using precise location of the borehole. We also demonstrated the extent of alteration of an assemblage by this bias using the information from our experiment. However, it is very difficult to use those simple criteria to evaluate natural time averaged assemblages. Hence we proposed some more general criteria to identify assemblages which were most likely underwent hydrodynamic sorting. Although many biased assemblages might not have any identifiable trace, these criteria will help workers to exclude assemblages which clearly are altered. Much more work is needed to document nature of bias across taxa, flow regimes. Bias may be present for some taxa but not others. For instance, since hydrodynamic behavior of gastropods is very different from bivalves (Statzner and Holm, 1989), it is possible to get a different contrast between drilled and undrilled gastropods than those of the bivalves. The same could be true for organisms which are very small, e.g. ostracods, foraminifera (Kontrovitch, 1975; Kontrovitch *et al.*, 1978; Kontrovitch and Snyder, 1981). In this study we discussed the results of the experiment with unidirectional flow. Future research should also evaluate the effect of oscillatory flow in more detail.

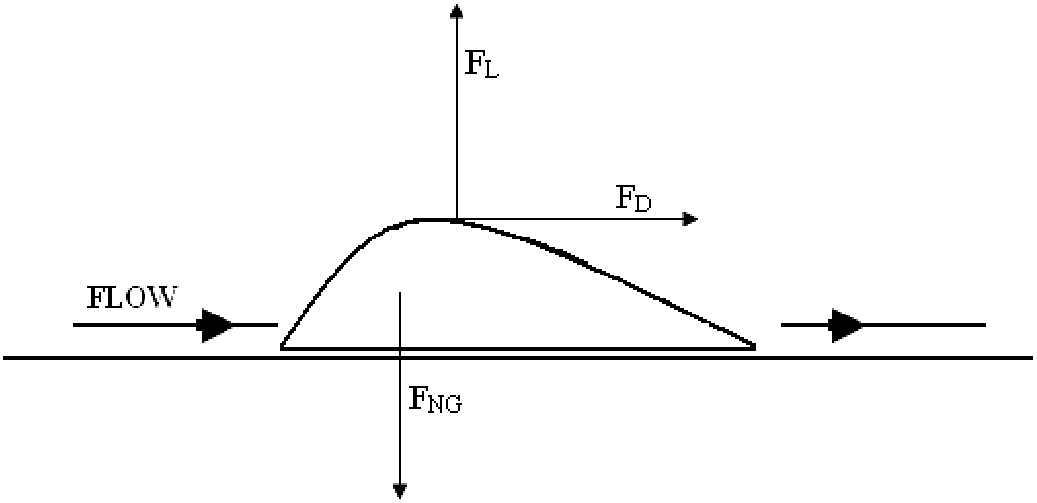

Figure 2.1: Schematic representation of forces acting on a single valve of a disarticulated shell immersed in a fluid flow.

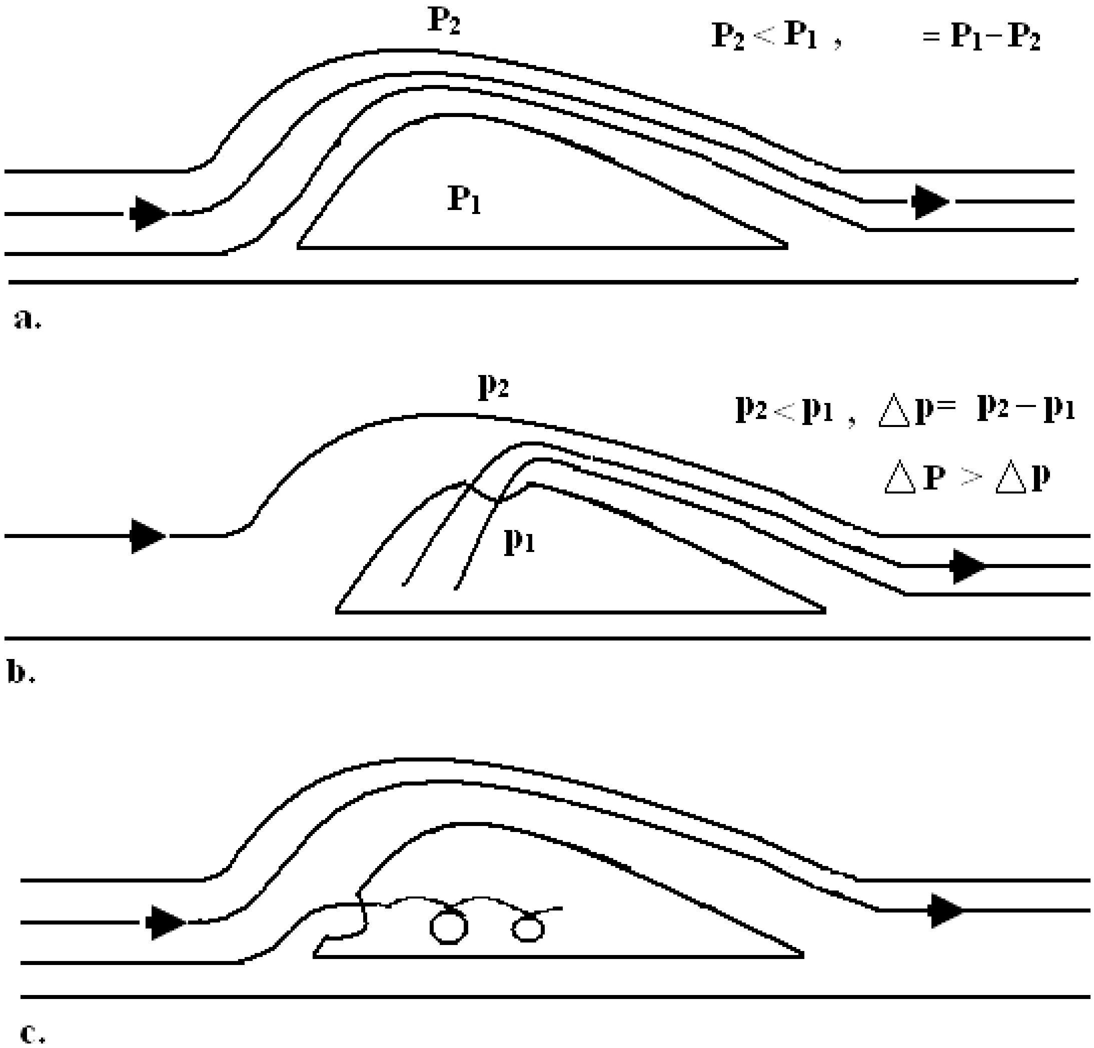

Figure 2.2: A schematic diagram showing the different patterns of fluid flow on a single valve of a disarticulated shell submerged in flowing fluid when a. the valve has no drill hole (P represents pressure), b. the valve has a centrally located drill hole (p re presents pressure), c. the valve has a umbonally located drill hole.

Figure 2.3: *Mulinia lateralis* valves with a. umbonally located drill holes, b. a centrally located drill holes.

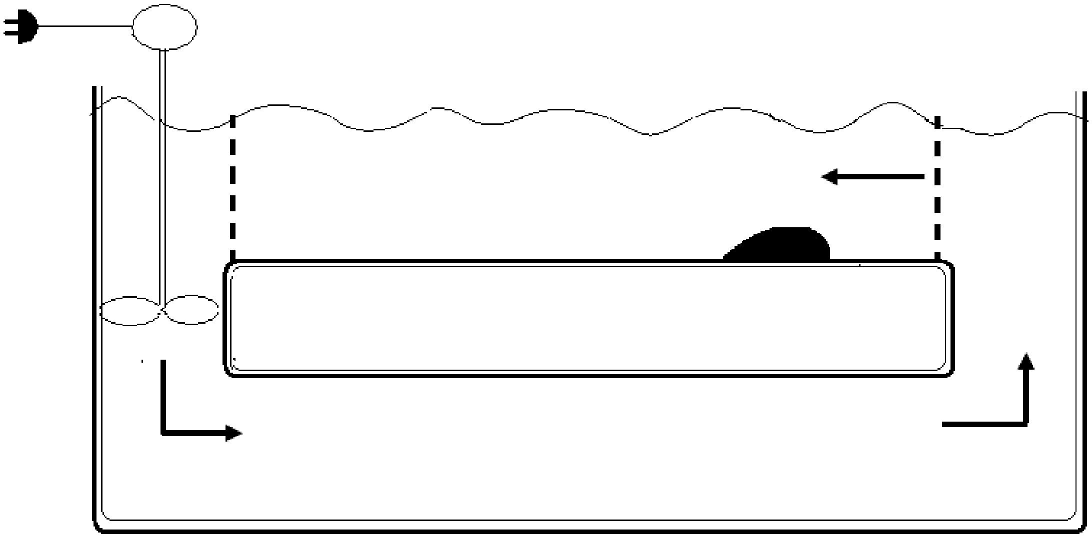

Figure 2.4: Schematic sketch of the flow tank used in the experiment.

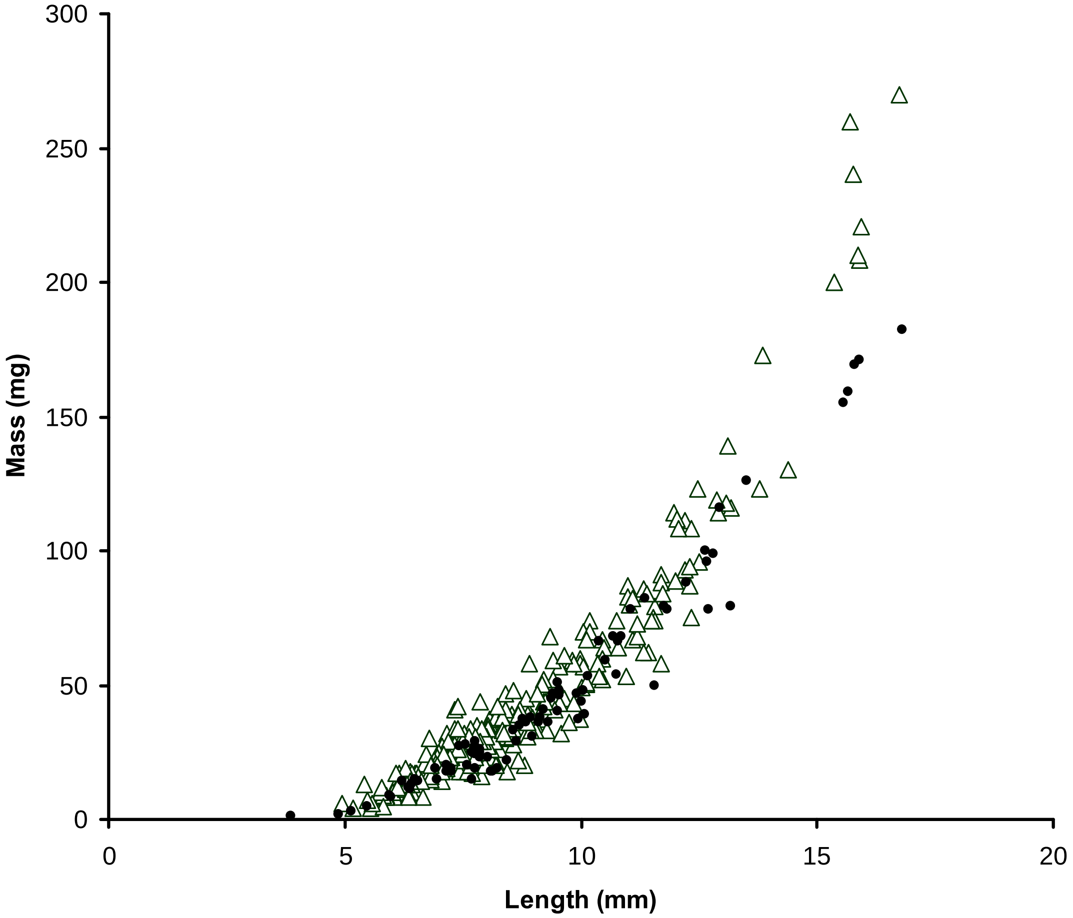

Figure 2.5: Plot showing the relationship between size and mass of drilled and undrilled valves. The solid circles represent drilled and the open triangles represent undrilled valves

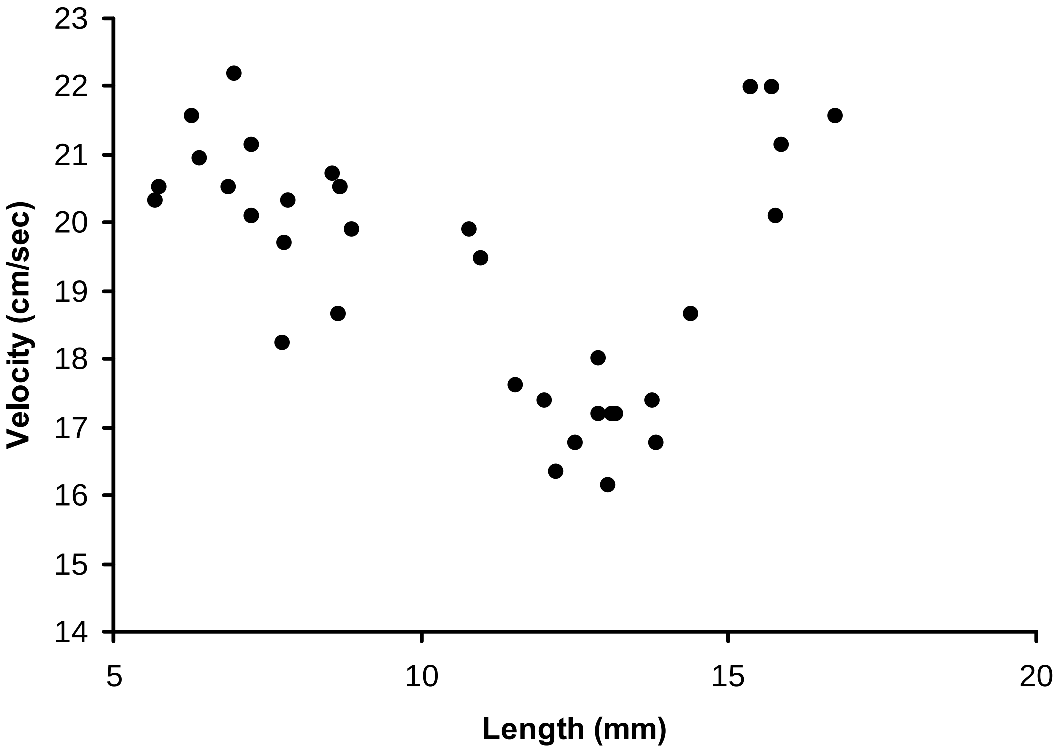

Figure 2.6: Plot showing the relationship between size and continuous entrainment velocity for undrilled valves.

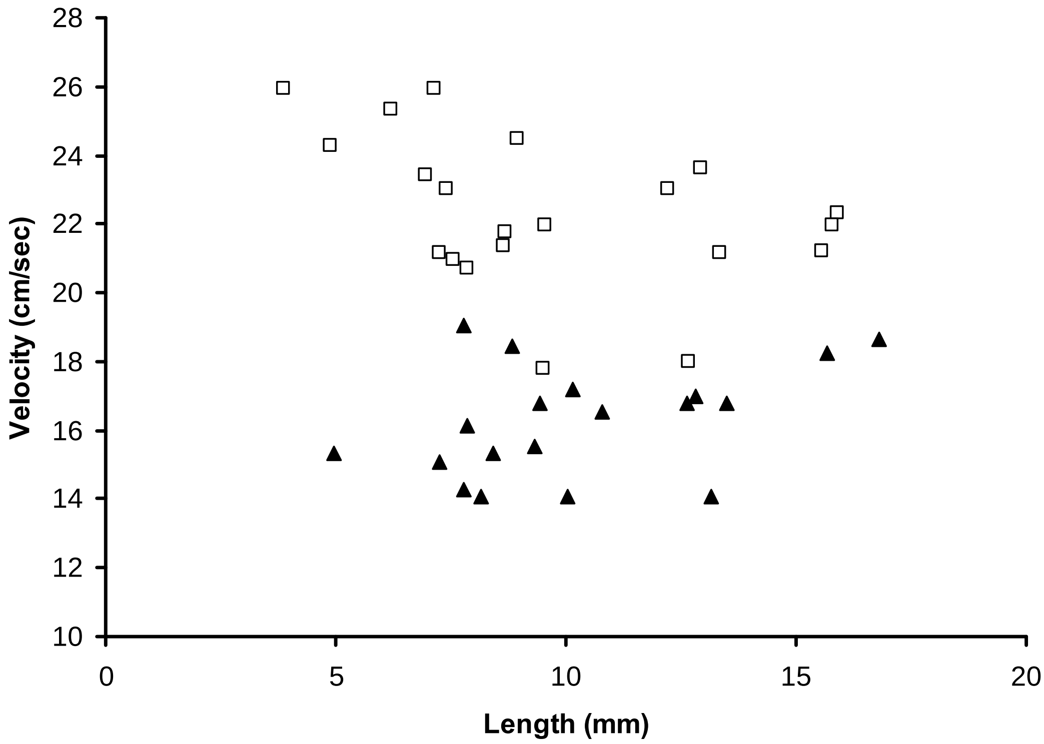

Figure 2.7: Plot showing the relationship between size and continuous entrainment velocity for drilled valves. The open squares represent centrally drilled shells and the solid triangles represent umbonally drilled shells.

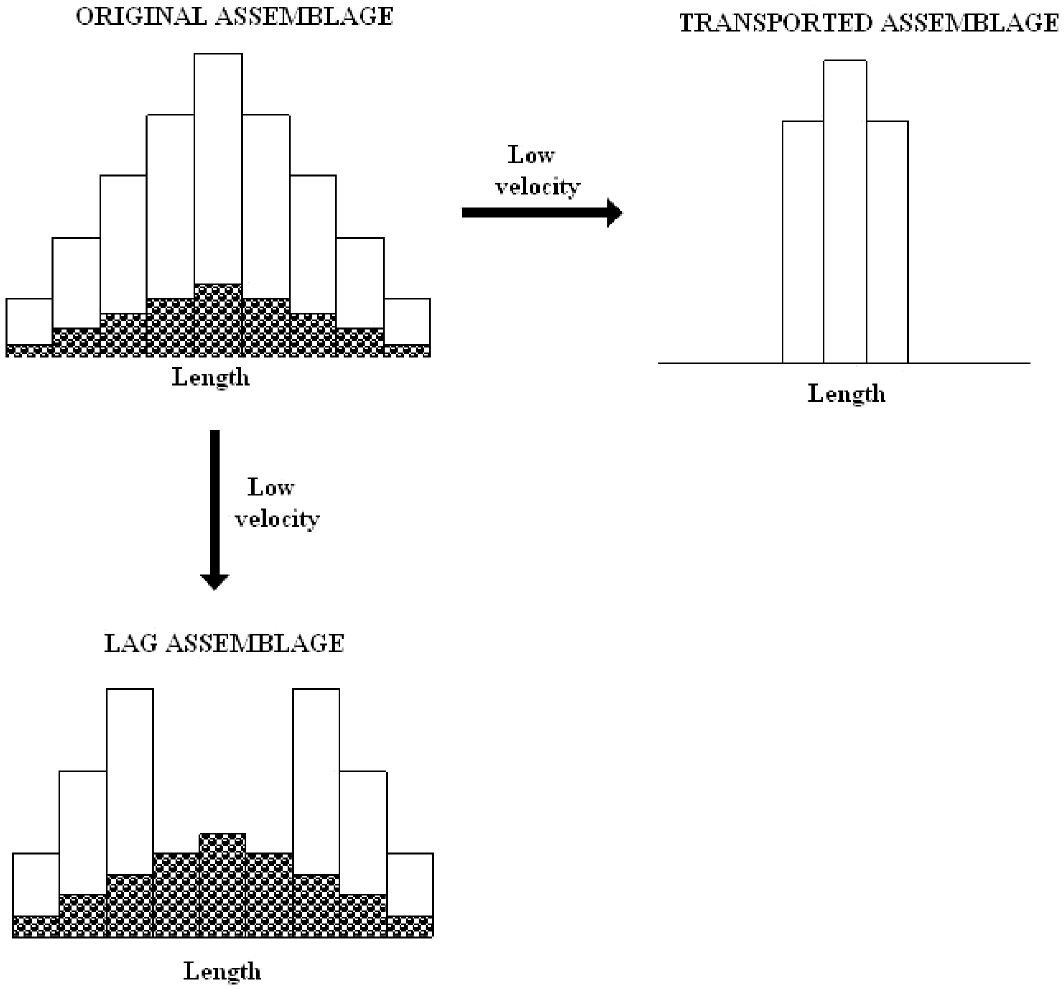

Figure 2.8: Diagram showing the distribution of centrally drilled and undrilled shells. White area represents undrilled shells and textured area represents centrally drilled shells.

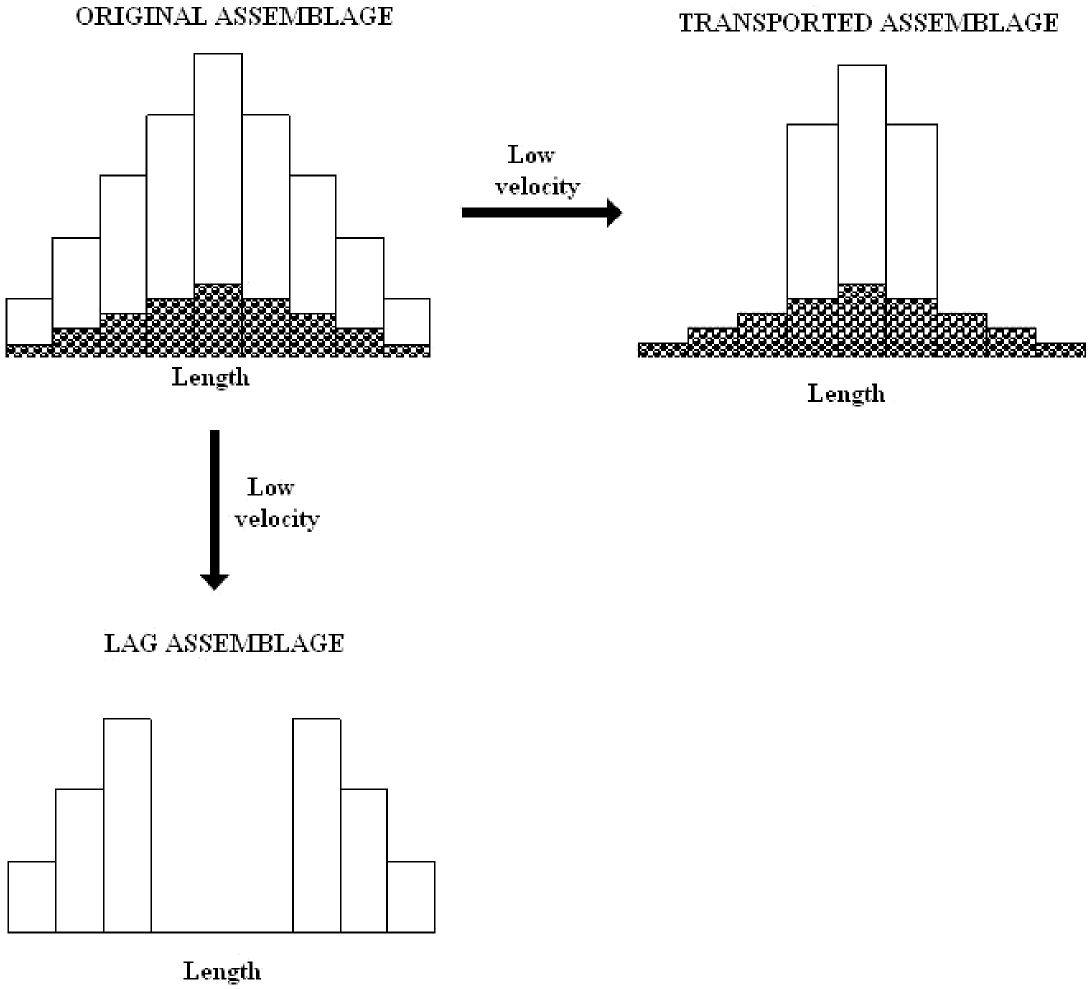

Figure 2.9: Diagram showing the distribution of umbonally drilled and undrilled shells. White area represents undrilled shells and textured area represents umbonally drilled shells.

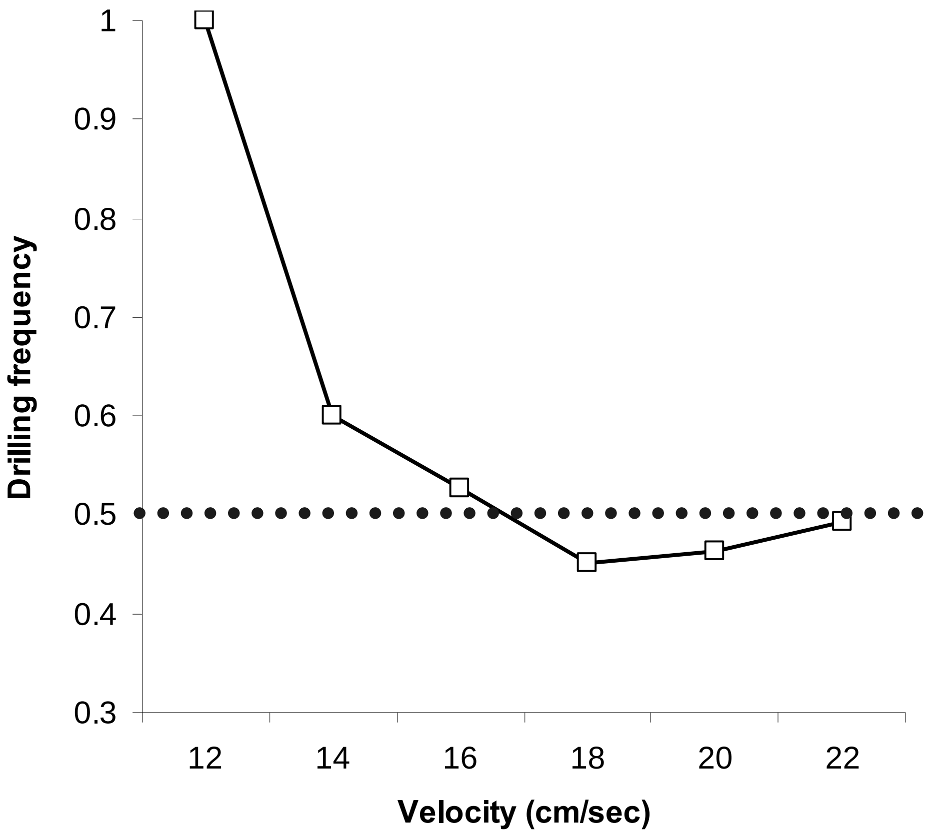

Figure 2.10: Plot showing the drilling frequency with different velocities in a transported assemblage. The dotted line represents true drilling frequency of the assemblage.

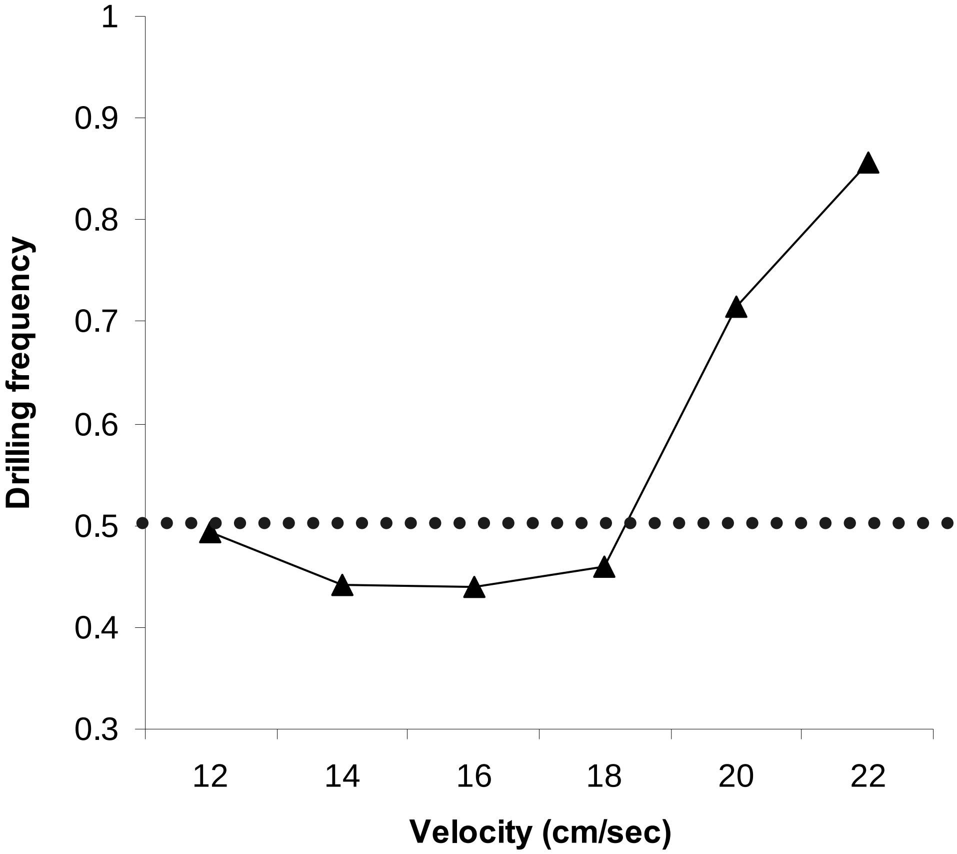

Figure 2.11: Plot showing the drilling frequency with different velocities in a lag assemblage. The dotted line represents true drilling frequency of the assemblage.

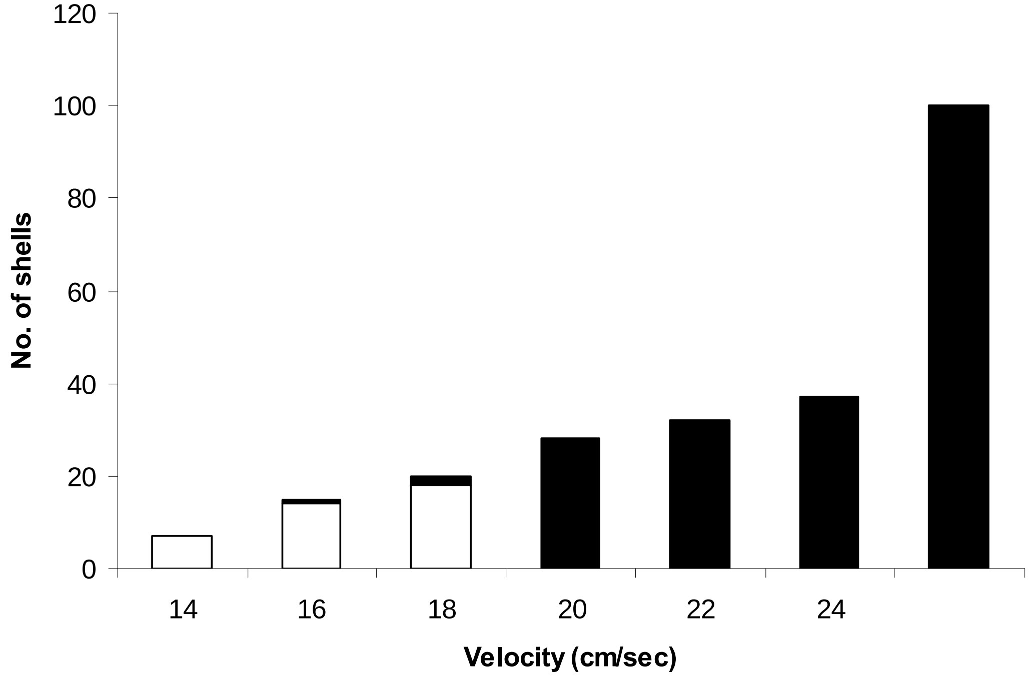

Figure 2.12: Plot showing the distribution of centrally and umbonally drilled shells with changing velocity in a transported assemblage. Centrally drilled shells are represented by black and umbonally drilled ones are represented by white.

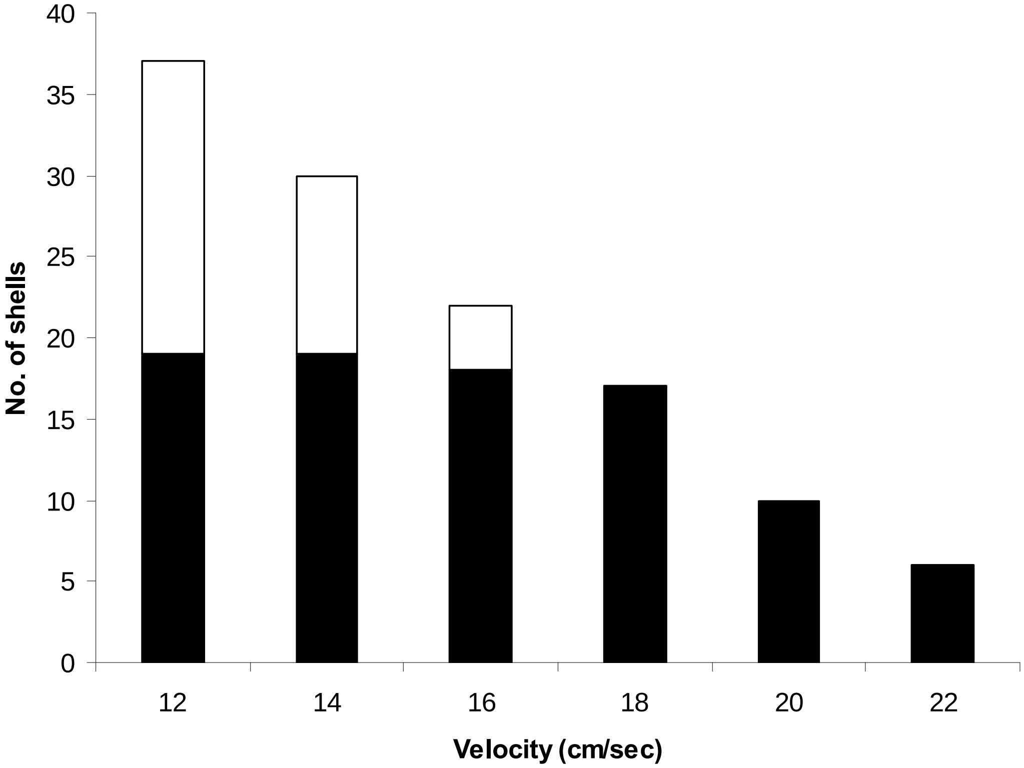

Figure 2.13: Plot showing the distribution of centrally and umbonally drilled shells with changing velocity in a lag assemblage. Centrally drilled shells are represented by black and umbonally drilled ones are represented by white.

CHAPTER 3

AN EXPERIMENTAL ASSESSMENT OF PENETRATION, EXCAVATION AND CONSUMPTION RATES OF THE MURICID GASTROPOD, *NUCELLA LAMELLOSA*

Introduction

The importance of ecological interactions in evolution has been a topic of some controversy. Evolutionary hypotheses like the concepts of coevolution and escalation assume that biological factors are major agents of natural selection and that organisms respond evolutionarily to selective factors imposed by other organisms, yielding arms races between evolving taxa (Dietl and Kelley, 2002). However, the importance of such factors in macroevolution has been questioned by some (Gould 1985, Madin et al, 2006, Madin et al, 2008).

What is uncontroversial is that in modern marine environments predation is an important ecological interaction and selective force with wide ranging consequences over ecological time scales. Assessment of the effects of predation over geologic time scales, while essential for paleoecological and evolutionary studies, has proven difficult, not least because most traces of predation are rarely preserved; most types of predation destroy the prey or leave no traces on the preservable hard parts of the victim. Predatory boring is an exception to this and represents one of the very few instances where the predator-prey systems of the past can be studied and analyzed quantitatively.

An important approach to understanding predator-prey systems has involved the study of energy, specifically, the energetic costs of predation and benefits (gains) from it; concepts such as Optimal Foraging Theory, are based on this approach (Krebs, 1977; Burrows & Hughes, 1991). For example, it has been demonstrated that the maximization of net energy gain is what governs the selection of prey by the predator (Kitchell *et al.*, 1981). Obviously, in order to evaluate drilling predation from the perspective of energetic costs, a good understanding of the mechanisms and estimates of rates of boring of hard tissue and consumption of soft tissue are essential. While both subjects have received some attention (Kitchell *et al.*, 1981, Rovero *et al.*, 1999; Navarro *et al.*, 2002), the aim of this study is to explore them in more detail and to provide a more thorough understanding of mechanism and more data on boring (excavation and penetration) and consumption rates.

Boring rate:

A variety of approaches have been used to study how and how fast predatory gastropods penetrate shells of their prey (Summary Table 3.1). Seminal studies by Carriker & Van Zandt (1972a, b) revealed that boring by muricid gastropods through the shell of prey involves the close interplay of the proboscis, propodium and the accessory boring organ (ABO). Carriker & Van Zandt (1972a) demonstrated that individuals from which the proboscis and radula had been amputated could recover, fully regenerate the proboscis, and resume boring after the radula and associated structures were formed and functional. Since gastropod boring involves the use of structures that increase in size during ontogeny, it is not surprising that most studies have found the diameter of bore holes to increase as a function of predator size (e.g., Kitchell *et al.*, 1981). Such a relationship implies that in order to penetrate the shell to a given depth, a larger gastropod must also remove a greater volume of shell material. If the rate of removal of shell material, henceforth referred to as "excavation rate" and measured in mg/hr, were independent of gastropod size, the rate of penetration (depth/time) ought to decrease with gastropod size. Apparently it is that assumption--that excavation rate is independent of gastropod size—that lead Kitchell *et al.* (1981) to predict that "[boring] time would increase with predator size" (p. 537, Kitchell *et al.*, 1981), However, Kitchell *et al.* (1981) provided no theoretical or empirical basis for such an assumption, and given that larger structures typically gain a mechanical advantage, one might expect that excavation rate ought to increase with gastropod size. In fact, the results of Kitchell *et al.* (1981) indirectly confirm that excavation rate varies with predator size, because, "Boring rates…revealed a consistent rate of penetration (mm h^{-1}) regardless of predator size" (p. 537).

Unfortunately, Kitchell *et al.* (1981) only provided data on rates of penetration (synonymous to "boring" and "drilling" in Kitchell *et al.* usage), somewhat preventing a quantitative assessment of how excavation rate varies as a function of predator size. In this study, we return to this question using experiments with the muricid gastropod *Nucella lamellosa* as drilling predator and the mussel, *Mytilus trossulus*, as prey.

Consumption rate:

Only a few studies have reported rates of soft tissue consumption by predatory naticid and muricid gastropods (Summary Table 3.2). Often the results of these studies are not comparable because the definitions of "consumption" (or "ingestion", as used by some authors) differ; in some studies it was defined as time needed for boring and consumption combined, whereas in others consumption time was the time of consumption of soft tissue after penetration of the shell. To avoid confusion, in this study we use the term "consumption" to indicate only the process of soft tissue consumption. Since we know of no published data on consumption rate of soft tissue as a function of predator/prey size, in this study we also tackled this problem using the two taxa described above.

Materials and methods

This study was conducted at Friday Harbor Laboratory (San Juan Island, Washington, USA) as part of a series of experiments on the behavior of drilling gastropods, their prey (mussels) and predators (crabs). A detailed description of Materials and methods can be found in Chattopadhyay and Baumiller, 2007; here we provide only a summary.

Specimens of the gastropod *Nucella lamellosa* and the mussel *Mytilus trossulus* were collected from False Bay, San Juan Island (Fig.3.1). Although *N. lamellosa* are abundant at False Bay, mussels are more difficult to find, but have been shown to be part of *N. lamellosa* diet (Kowalewski, 2004), and we found several bored mussels at this locality.

Gastropods, when brought in from the field, were placed in a flow-through sea water table and left without food for a minimum of one week. Mussels were kept in separate sea water tables until needed for the experiment. It has been previously shown that temperature and salinity have an effect on gastropod feeding rates (Hanks 1957;

Manzi 1970; Farrell 2004), therefore both were closely monitored and maintained in the proper range in all tables throughout the duration of the study (mean temperature 16ºC±3ºC and salinity 29 ‰ ±1).

Experimental design and procedure:

A large number (N= 100) of *Mytilus trossulus* were placed in a sea table (dimensions 127cm x 66cm x 20cm) with a steady and continuous flow of sea water. Barnacles, limpets and other epibionts were removed from the mussels by careful scraping with a blunt knife to reduce the effect of epibionts or encrusters on susceptibility to predation. Mussels that were damaged during this procedure or heavily encrusted mussels were not used. We separated the mussels from each other because clumping behavior has been shown to inhibit predators that need to orient their prey during attacks (e.g., Bertness and Grosholz 1985, Cote and Jelnikar 1999, Casey and Chattopadhyay, 2008).

Experiment was started simultaneously by randomly placing an equal number (N=100) of specimens of the predatory gastropod *Nucella lamellosa* in the table. A black grease pencil was used to mark each gastropod so that their behavior could be monitored and they were allowed to hunt freely. Whenever a gastropod latched onto a mussel, both predator and prey were isolated by using a plastic mesh cage (for detail see Chattopadhyay and Baumiller, 2007). Time from latching through consumption and release was used as an estimate of handling and boring time. We monitored the sea tables for approximately 30 minutes every three hours during daylight hours only (6am-9:30pm). No observations were made at night (9:30pm-6am). The only data that might have been affected by lack of observations at night would be for boring time, therefore when estimating boring time, we used maximum and minimum time estimates (See Appendix, Table 3.4).

When a mussel had been abandoned with an incomplete drill hole or killed, it was removed from the sea table and replaced by one of similar size. The snail responsible for that attack was measured and then allowed to continue hunting. Mussels that had considerable soft tissue left inside after an attack were preserved in alcohol; those with little or no tissue were washed and preserved.

Data acquisition:

Measurements of boring rates were obtained by utilizing only incompletely bored specimens. While for naticids it is easy to pinpoint the initial phase of boring because the predator becomes infaunal with its prey (Kitchell *et al.*, 1981), muricids do not show any such drastic movement in the initial phase. Therefore, we defined the initiation of boring as the time of latching of the snail onto the mussel; the abandonment of an incompletely bored mussel marked the end of boring. Because no observations were made at night, boring time (T_{bore}), the time between initiation and end of boring was estimated following a protocol described in the Appendix (Table 3.4 and Fig. 3.10). For incompletely bored specimens, silicone molds of the bore holes were made (Fig. 3.2), photographed using an optical microscope, and their maximum relief (equivalent to depth of penetration, d), diameter, and volume (Vol) were obtained using digitization software Image J. As a cross check, bore hole diameter was compared with published data on bore hole diameter and snail size (Kowalewski, 2004). These data were used to estimate rates of penetration (d / T_{bore}) and excavation (Vol / T_{bore}).

Measuring rates of consumption of soft tissue required a number of steps. First, a relationship between dry soft tissue mass (DSTM) and size of mussel had to be established. To do this, different sized specimens were placed in an oven at 65ºC where they remained for 6 to 12 hr until they achieved constant mass, this is their dry mass (DM); subsequently, they were placed in a muffle furnace at 500ºC for 3 hours and weighed to the nearest 0.001mg to obtain their skeletal mass (SM). Dry tissue mass (DSTM) was calculated as the difference between dry mass and skeletal mass (DSTM = DM-SM). Specimens were massed using a Mettler H6 electronic balance.

Using the relationship between size and dry soft tissue mass (DSTM) from above, the soft tissue mass removed by the predator from a given sized bored, completely consumed mussel, could be estimated. In these completely bored and consumed specimens, boring time (T_{bore}) could also be estimated as the ratio of the depth of the bore hole to the previously established penetration rate. For each of these specimens, the difference between the total time from latching to abandonment and the expected boring time represents the time taken for consumption ($T_{consumption}$). Consumption rate is the ratio of dry tissue mass to consumption time (Consumption rate = $DSTM/ T_{consumption}$)

(Appendix Table 3.5, Approach 1). We also calculated the consumption rate by another method (Appendix Table 3.5, Approach 2) and the results are comparable.

Results

Using the incompletely bored mussels from the sea table, the calculated penetration rate was 0.013 ± 0.002 mm/hr (Fig. 3.3).

While penetration rate is independent of snail size (Fig. 3.4), excavation rate, i.e., volume of shell material removed per unit time, is positively correlated with snail size ($p<0.05$) (Fig. 3.5). Even after the two outliers in the data set were excluded, it remained significant.

Using the penetration rate data and the standard mass equation for *Mytilus trossulus* (Appendix Fig. 3.11), the consumption rate (6.25 mg/hr) for the mussels was calculated (Fig. 3.6). Like excavation rate, the consumption rate is positively correlated with snail size ($p<0.05$) (Fig.3.7) and weakly correlated with mussel size (Fig. 3.8) (Table. 3.3).

Discussion

Our results on penetration rates are comparable to previously published results (Table 3.1), but they add an interesting twist to a previous study by Kitchell *et al.* (1981). As mentioned in the Introduction, Kitchell *et al.* (1981) claimed that “drilling time would increase with predator size in direct proportion to the volume of shell material removed, i.e., the geometry of the borehole”, implicitly assuming that the rate of excavation (volume of shell material removed/time) was independent of the size of the predator and the size of its boring organ. This assumption was not justified, made little sense on biomechanical grounds, and their data refuted their claim: penetration rate (~ boring time for shells of equal thickness) was found to be independent of predator size, which meant that excavation rate MUST have increased with predator size (because the diameter of the bore holes increases with size). Using data from two previous studies (Kitchell *et al.*, 1981; Kardon, 1998), we determined the excavation rates and it increases with predator size as we have predicted (Fig. 3.9).

Shell penetration involves an intricate chemical-mechanical process in which the ABO secretes a substance dissolving the shell at site of penetration and a minor portion of the partly dissolved shell is removed by the radula and swallowed (Carriker and Van Zandt, 1972b). According to Carriker and Van Zandt (1972 a, b), borehole morphology is the product mainly of dissolution. As a result, the form and size of the bore hole generally mirror the shape and size of the secretory disc of the ABO. Carriker and Van Zandt (1972a, b) also suggested that the maximum depth of the bore hole is dependent on the size and shape of the secretory disc of the ABO. Since, ABO is the main agent in shaping the morphology of a bore hole, Carriker and Van Zandt (1972b) found the average diameter of exterior opening of the borehole to be a reliable proxy of the size of the normal functional ABO. In this study we empirically measured excavation and penetration rates and found the former to be positively correlated to snail size, and the latter independent of snail size. The increase in excavation rate with increasing snail size is perfectly compatible with the fact that large snails have a larger ABO (inferred from the lager outer diameter of borehole) and that this organ must possess some advantage, if only because of its greater volume of muscle. What is surprising is that the obvious ontogenetic increase in size (length, diameter, volume) of the boring organ, still results in a constant rate of penetration, as illustrated by this and other studies.

Our data on consumption rate are also comparable with the results of several other studies (Bayne & Schuller, 1978; Burrows and Hughes, 1991). However, our results on the relationship between consumption rate and predator size differ from the results of previous authors, and might have important consequences for cost-benefit analyses. For example, Kitchell *et al.* (1981) reported that the "ratio of drilling time: ingestion time for the preferred prey, *Mya*, is approximately 1.0. For *Mercenaria* this ratio was 2.4, and for *Chione* it was 4.9." This implies that either (1) boring and consumption rates varied in exactly the same proportion with the size of the predator, or (2) both were constant. Given that Kitchell *et al.* (1981) found boring rates to be independent of predator size in their experiments, explanation (2) must have been true, i.e., consumption rates were constant and independent of predator size. Our empirical results contradict this finding: consumption rates vary directly with predator size, as one might predict on biomechanical grounds—larger organisms are capable of faster consumption.

In assessing prey preferences using a cost-benefit approach Kitchell *et al.*, (1981) relied on penetration rates alone, ignoring rates of consumption. Yet as our data on rates of penetration, excavation and consumption suggest, the latter is not insignificant and should be considered in cost-benefit analyses and optimal foraging theory studies.

Predator		Prey	Drilling rate (mm./hr)	Method	Reference
Naticid	*Lunatia nitida*	*Angulus fabula*	0.025	Direct observation of drilling.	Ziegelmeir, 1954
	Polinices duplicatus	*Mya, Polinices, Mercenaria*	0.022	Interruptions of drilling at known time intervals.	Kitchell *et al.*, 1981
	Neverita duplicate	*Corbula gibba*	0.0126	Interruptions of drilling at known time intervals.	Kardon, 1998
Muricid	*Murex erinaceus*	*Cardium*	0.012-0.013	Direct observation of drilling.	Piéron, 1933
	Murex erinaceus	*Tapes*	0.007-0.012	Direct observation of drilling.	Piéron, 1933
	Nucella lapillus	*Mytilus edulus*	0.014	Direct observation of drilling	Ziegelmeir, 1954
	Urosalpinx cinerea	*Crassostrea virginica*	0.0135, 0.0129	Recording scraping sound.	Carriker & Van Zandt, 1972b
	Nucella lapillus	*Mytilus edulus*	0.012	Automatic long-term recording of radular rasping.	Rovero *et al.*, 1999
	Nucella lamellosa	*Mytilus trossulus*	0.015	Interruptions of drilling by secondary predator.	This study

Table 3.1: List of studies on drilling rate.

Predator		Prey	Consumption rate	Definition	Reference
Naticid	*Polinices duplicatus*	*Mya, Polinices, Mercenaria*	Drilling: Consumption Time Mya: 1.0 Merceneria: 2.4 Chione:4.9	Time to consume the prey after penetration	Kitchell *et al.*, 1981
	Chorus giganteus	*Mytilus chilensis* *Tagelus dombeii*	Temp. mg h^{-1} ind $^{-1}$ 18C 0.17 15C 3.32 13C 9.6 15C 24.6	Total time to consume the prey	Navarro et al, 2002
	Thais lapillus	*Mytilus edulis*	Temp mussels/day 9C 0.25 15C 0.28 20C 0.38	Drilling+ Consumption	Bayne & Schuller, 1978
Muricid	*Nucella lapillus*	*Mytilus edulis*	Penetration + Consumption 10 tidal cycle	Time to consume the prey after penetration	Burrows and Hughes, 1991
	Nucella lamellosa	*Mytilus trossulus*	6.25 mg h^{-1}	Time to consume the prey after penetration	This study

Table 3.2: List of results of the studies on consumption rate.

Y	**X**	***t***	**P-value**
Drilling rate	Snail size	0.73	0.48
	Mussel size	-1.36	0.19
Excavation rate	Snail size	2.53	0.02
	Mussel size	-2.03	0.06
Consumption rate	Snail size	2.58	0.04
	Mussel size	1.53	0.08

Table 3.3: Statistical test results.

Figure 3.1: Location map of False Bay in San Juan Island, WA, USA.

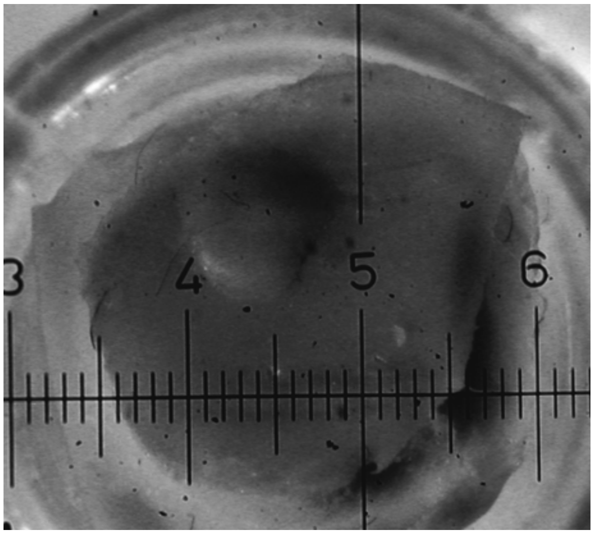

Figure 3.2: Silicon mould of an incomplete borehole used for the depth measurement.

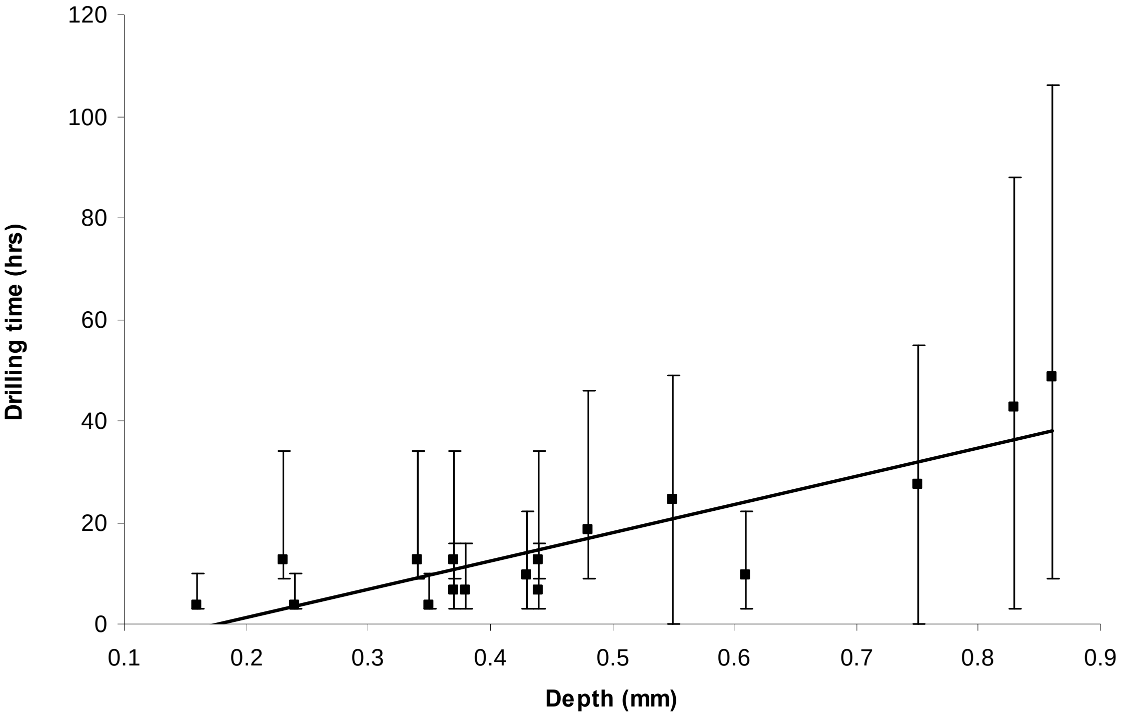

Figure 3.3: Plot showing the relationship between depths and drilling time for the incompletely drilled mussels, collected from the experimental table.

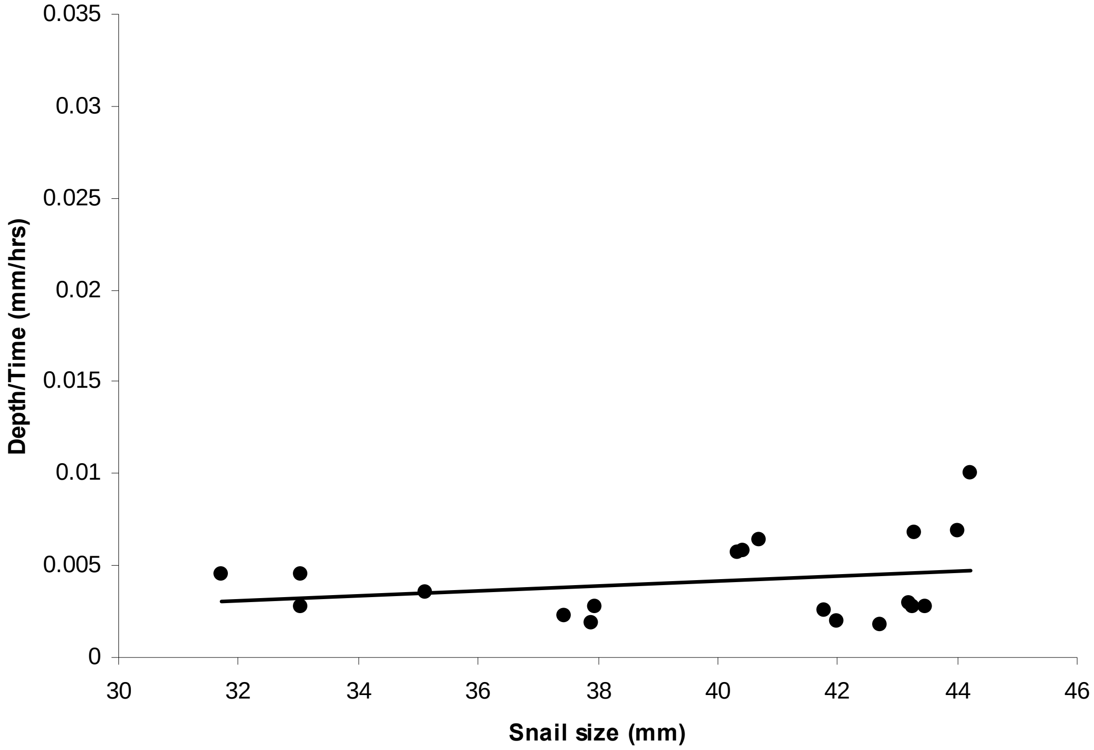

Figure 3.4: Plot showing the relationship between snail size and penetration rate for the drilled mussels.

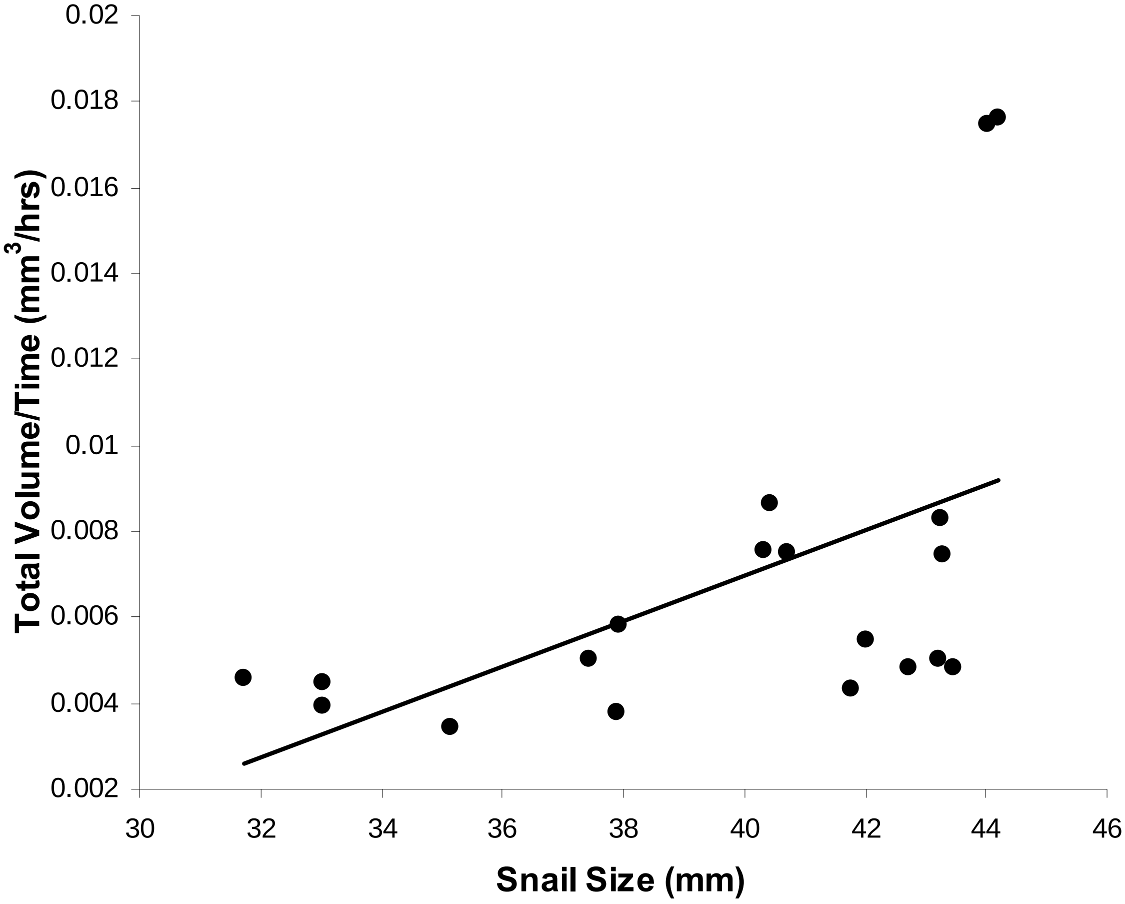

Figure 3.5: Plot showing the relationship between snail size and excavation rate (y = 0.0005x - 0.0141, R^2 = 0.2736).

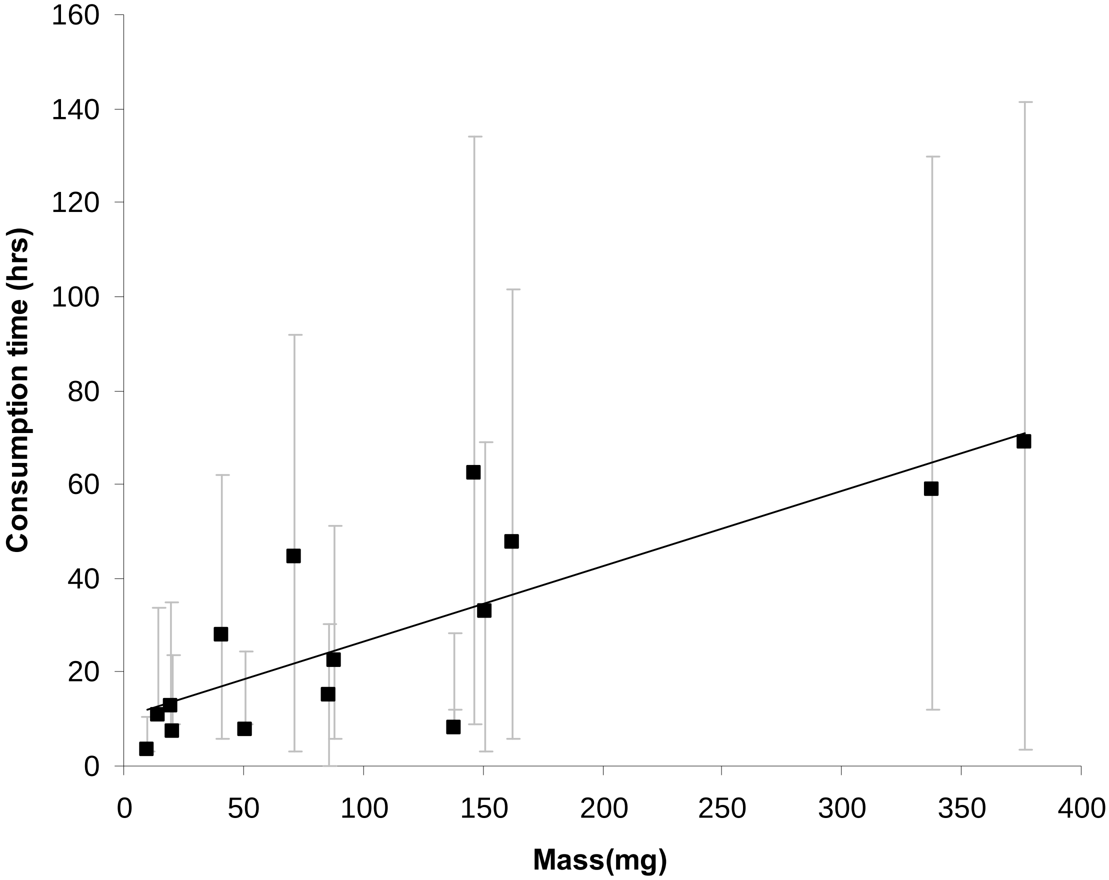

Figure 3.6: Plot showing the relationship between mass of the mussel and the consumption time.

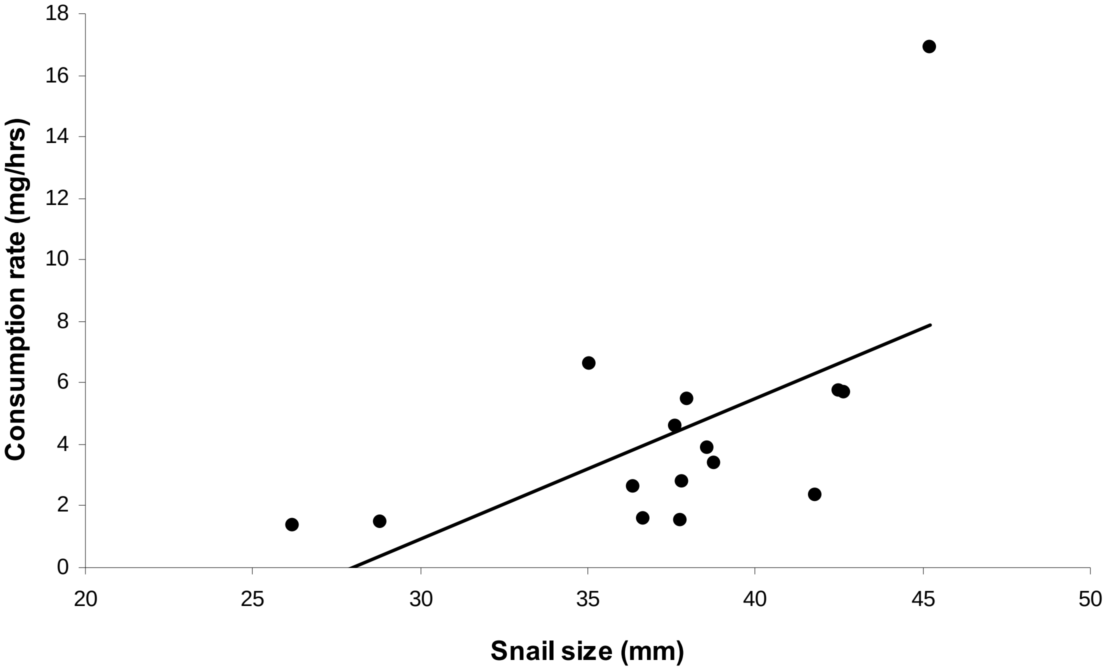

Figure 3.7: Plot showing the relationship between snail size and consumption rate ($y = 0.4567x - 12.761$, $R^2 = 0.339$).

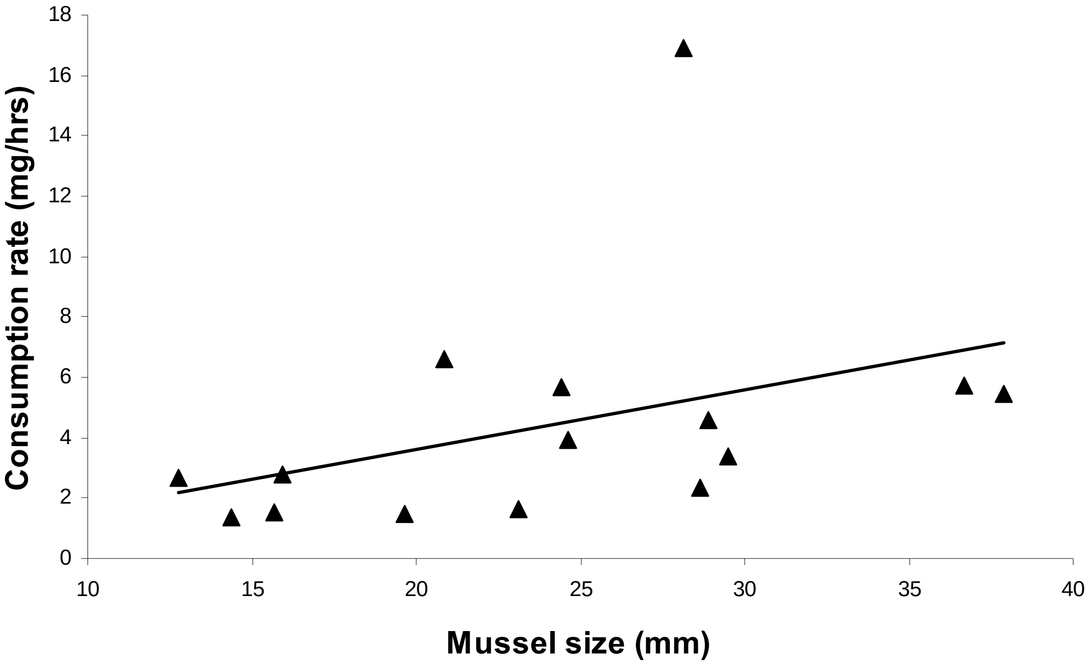

Figure 3.8: Plot showing the relationship between mussel size and consumption rate (y = 0.1975x - 0.3533, R^2 = 0.153).

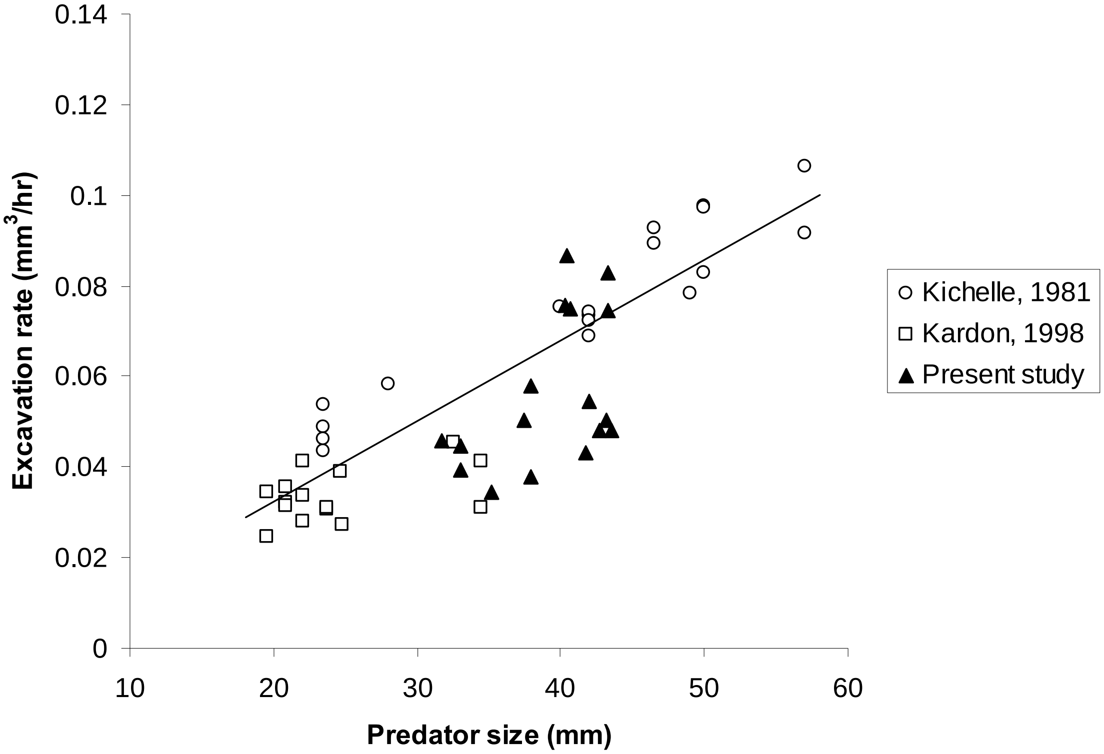

Figure 3.9: Plot showing the relationship between predator size and excavation rate based on this study and published literature data.

Appendix:

Cases	Start (a)	Finish (b)	Time (T)	Maximum (hrs.)	Minimum (hrs.)
1	6am	9am/12am/3pm/6pm/9pm	b-a	T+8.5	T-3
2	6am	9:30am/pm	b-a	T+8.5	T-0.5
3	9am/9pm	9:30am/9:30pm	b-a	T	T-0.5
4	9:30 am	12am/3pm/6pm/9pm	b-a	T+0.5	T-3
5	9:30 am	9:30 pm	b-a	T+0.5	T-0.5
6	9am/12am/3pm/6pm	9pm	b-a	T+3	T-3
7	9am/12am/3pm/6pm/9pm	9:30pm	b-a	T+3	T-0.5
8	9am/12am/3pm/6pm/9pm	6am *	b-a	T+11.5	T-8.5
9	9:30am/9:30pm	6am *	b-a	T+9	T-8.5

* Time recorded not in the same day of starting.

Table 3.4: Summary of the protocol maintained when estimating the maximum and minimum time for each predation attempt.

<table>
<tr><td rowspan="2">Approach 1</td><td>Size</td><td colspan="2">Thickness at the drillhole</td><td>Expected drilling time</td><td>Total time</td><td>DSTM of sample</td><td>Consumption rate</td></tr>
<tr><td>l</td><td colspan="2">d</td><td>$t=f(d)$</td><td>T</td><td>$M=f(l)$</td><td>$I=M/(T-t)$</td></tr>
<tr><td rowspan="2">Approach 2*</td><td>Size</td><td>Thickness at the drillhole</td><td>Expected DSTM</td><td>DSTM of sample</td><td>Total time</td><td>Expected drilling time</td><td>Consumption rate</td></tr>
<tr><td>l</td><td>d</td><td>$m= f(l)$</td><td>M</td><td>T</td><td>$t=f(d)$</td><td>$I= (M-m)/(T-t)$</td></tr>
</table>

Table 3.5: Summary of two different approaches, used for estimating consumption time.

* For the second approach, we measured the mass of partially eaten mussels and compared them with the untouched mussels of the same size. The difference in weight in them is the portion that has already been ingested by the predator. Using the drilling rate information, consumption rate was calculated.

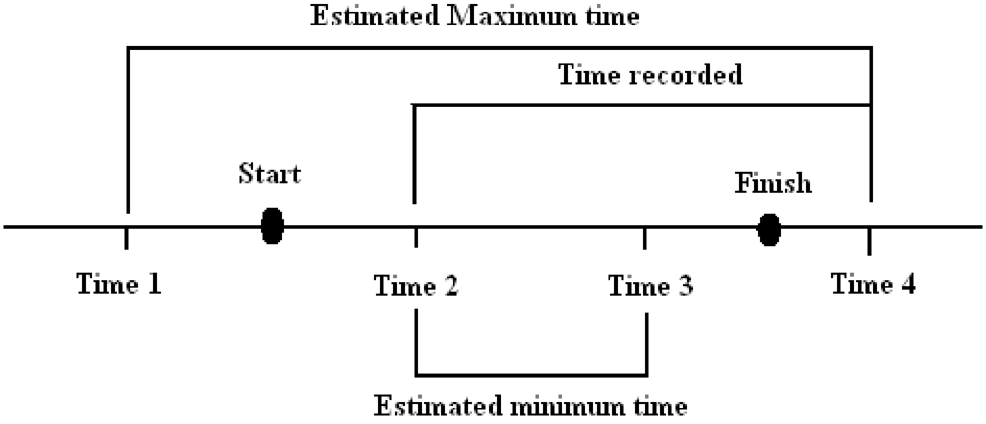

Figure 3.10: A schematic representation of the protocol. When estimating the maximum time, we assumed that the snail started drilling just after the last reading and finished when it was recorded. For estimating the minimum time for an event, we assumed that it started right before when it was detected and finished before it was actually recorded.

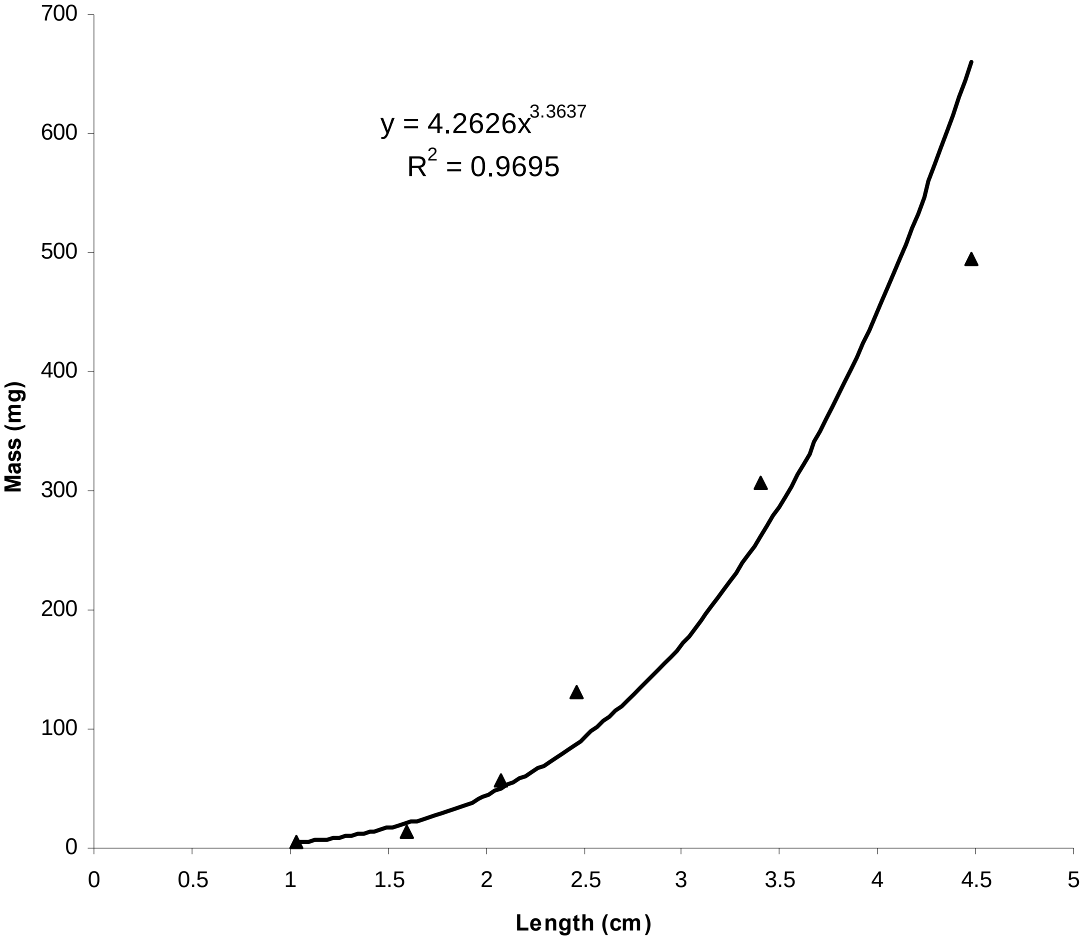

Figure 3.11: Relationship between length and dry soft tissue mass (DSTM) for *Mytilus trossulus*. The equation derived from this graph is: DSTM (mg) = 0.0018 + 3.3637 ln (Length (cm))

CHAPTER 4

DRILLING UNDER THREAT: AN EXPERIMENTAL ASSESSMENT OF DRILLING BEHAVIOR OF *NUCELLA LAMELLOSA* IN THE PRESENCE OF A PREDATOR

Introduction

In modern marine environments, predation is a significant agent of mortality. However, evidence of predation in fossils is generally rare, primarily because most predators destroy the prey or leave no traces on any preservable hard parts of the victim. Drilling predation of shelled marine invertebrates by muricid and naticid gastropods represents one of the very rare instances that allow biotic interactions to be evaluated quantitatively in the Recent and in the geologic record. Not surprisingly, drill holes have been used as an important source of information on the nature of biotic interactions and to explore the ecological and evolutionary roles of such interactions (Vermeij, 1987, Kelley & Hansen, 1993, Dietl & Herbert, 2002). For example, frequency of drill holes has been used to estimate predation intensity (Taylor, 1970; Stanton & Nelson, 1980;Vermeij *et al.*, 1980; Vermeij & Dudley, 1982; Kabat & Kohn, 1986) while frequencies of incomplete drill holes have been used as a measure of failed predation events (but see Kowalewski, 2004) and thus as an indicator of prey effectiveness (Kelley & Hansen, 2001). In this context, incomplete drill holes are thought to result when a predator abandons its prey because it failed to overcome the prey's defenses. However, prey abandonment could occur for reasons that have little to do with the effectiveness of the prey vis a vis the predator, for example when the driller is physically interrupted by an external agent such as its own predator, hence referred to as "secondary predator" (Kelley and Hansen, 2003). In fact, behavior of snails may be affected even by the presence of a secondary predator or the mere evidence of its predatory activities. Of course, the probability of being interrupted by a secondary predator may be a function of prey effectiveness such as when the prey is thicker-shelled, requiring more drilling time and thus increasing the probability of interruption.

An example of the effect of secondary predators has been reported for the Recent mud snail *Nassarius obsoletus* by Atema and Burd (1975). These authors demonstrated that whereas normally the snails scavenge crushed mussels and snails, they depart rapidly when placed in the vicinity of crushed conspecifics. In other studies, it has been shown that snails responded negatively to the presence of crushed conspecifics, but that their escape response was diminished by hunger (Stenzler & Atema, 1977; Morton & Chan, 1999).

If the mere presence of a secondary predator or of its activities can threaten the driller and cause abandonment, the frequency of incomplete drill holes could vary as a function of the presence of secondary predators rather than prey effectiveness. Even the threat of a secondary predator might affect drilling frequency and thus have consequences for interpreting predation intensity.

The present study was designed to asses the effect of threat of a secondary predator on the drilling behavior of a muricid gastropod, including its effect on incomplete drill hole frequency and overall drilling frequency.

Materials

The experiments were conducted at Friday Harbor Laboratory (San Juan Island, Washington, USA). Specimens of the gastropod *Nucella lamellosa* and the mussel *Mytilus trossulus* were collected from nearby False Bay. False Bay is a semicircular bay on the west side of San Juan Island (Fig.4.1) with a substrate of fine sand and mud surrounded by a rocky shoreline. The island has a tidal range of about four meters, enough to cause near total exposure of False Bay at low tide and total immersion at high tide. Both species were collected from rocks and tide pools in the SSE side of the mouth of the bay. *Nucella lamellosa* are particularly abundant at False Bay, whereas mussels are quite rare. *Nucella lamellosa* probably prey primarily on barnacles but it has been shown that mussels are also part of their diet (Kowalewski, 2004) and, while collecting live specimens, six drilled mussels were recovered from this locality. The crab, *Cancer gracilis,* collected during a dredge trip, was selected as a secondary predator; *C. gracilis* is relatively common in False Bay and live specimens of *Nucella lamellosa* collected for the experiments often possessed repair scars, suggesting that they were frequently attacked by durophages such as *Cancer gracilis* in their natural habitat (mean temperature 20^{o} C and salinity 27‰).

. After collection, the gastropods were placed in a flow-through sea water table and left without food for a minimum of one week. There was no attempt of cannibalistic drilling observed when the snails were in the sea table. The mussels and crabs were kept in two separate sea water tables until needed. All water tables had a constant flow of seawater.

Experimental design

To study the effect of the presence of the crab on gastropod drilling behavior, two sea tables with identical dimensions (127cm x 66cm x 20cm), water levels and with a steady and continuous flow of sea water were used. Each sea-table contained 100 individuals of *Mytilus trossulus*, from which barnacles, limpets and other epibionts had been removed by careful scraping with a blunt knife to reduce the effect of epibionts or encrusters on susceptibility to predation. Mussels damaged during this procedure or that were heavily encrusted were not used in the experiment.

A total of 200 specimens of *Nucella lamellosa* were divided into two groups of 100 individuals each. Each individual was marked using a black grease pencil so that their behavior could be monitored.

In both sea tables, roughly 1/6 of the area on the upstream side was separated from the rest by a plastic mesh that allowed free flow of water. In that enclosed upstream area of one sea table (“experimental table”), one crab was introduced twice daily, at 12 hour intervals for 30 minutes. At the same time, 2 crushed *Nucella lamellosa* were also placed on the upstream side of the enclosed part in the experimental table. The other sea table (“control table”), without the crab and the crushed snails, served as a baseline for the experiment. In the initial phase of the experiment we tried introducing the crab and the crushed snails separately. There was no significant difference between the effects. We observed that the combined effect was much stronger. So we decided to introduce them together.

Experiments in both tables were started simultaneously by random introduction of 100 predatory gastropods at densities approximately corresponding natural densities which were allowed to hunt freely. The mussels were separated from each other to prevent clumping, as clumping behavior has been shown to inhibit predators that need to orient their prey during attacks (e.g. Bertness and Grosholz 1985, Cote and Jelnikar 1999). Whenever a gastropod latched onto a mussel, both predator and prey were isolated by using a meshed plastic cage. We wanted to monitor the effect of the presence of secondary predator on the snail's drilling behavior. After latching onto a mussel if they were not separated from the rest of the snails, most frequently they were disturbed by other snails. In that case it would have been really difficult to recognize whether the effect was a result of the disturbance caused by conspecific or a secondary predator. Use of the plastic cage solved the problem. Secondly, although we marked the snails, during the drilling sometimes they orient themselves in such a way that it is impossible to see their marking. So it was much easier to identify them once and mark their cage with the same number. That way every time when taking a reading, we did not have to look for the mark on the snail. Time from latching through consumption and release was used as an estimate of handling, drilling and feeding time. The tanks were monitored every three hours during daylight hours (6am-9:30pm). Detailed observations of the snails and mussels were also made just prior to the introduction of the crab and 30 minutes after it had been introduced. There was no observation made at night (9:30pm-6am).The only data that might have been affected by lack of observations at night would be for drilling time. When estimating drilling time, we considered the factor and calculated the maximum or minimum estimate. Temperature and salinity in both sea tables were monitored throughout the duration of the experiments (mean temperature 16^{o} C±3 ^{o} C and salinity 29 ‰ ±1 ‰)

When a mussel was killed or abandoned with an incomplete drill hole present (Fig. 4.2), it was removed from the sea table and replaced by one of similar size. If the mussel retained considerable soft tissue, the specimen was preserved in alcohol (99%). Otherwise the mussel was washed and dried.

Results

Impact on overall drilling frequency:

Snails in the two sea tables attacked a total of 181 out of 324 individuals of *Mytilus trossulus* (Table.4.1). Fatal attacks, where the snail killed and consumed (fully or partially) the soft parts inside the mussel, were considered successful. Success rates were significantly different in the two tables. In the experimental table, 26% of the attacks were successful (24 dead mussels), whereas in the control table 89% of the attacks were successful (79 dead mussels) (p<<0.05). Of all successful attacks, 97% involved drilling: one dead *Mytilus* from the control table and three from the experimental table were found without a drill hole. The shells of the four victims without drill holes were gaping. The one from the control table had no soft tissue left, whereas the three mussels from the experimental table had some soft tissue inside, as the snails abandoned them when the crab was introduced. Since no edge drill holes or other damage to the shells was detected, it would be impossible to identify them as victims of successful predation without having observed the attacks. Although in the experimental table successful attacks without drilling were more common, the difference between the tables was not statistically significant.

During unsuccessful attacks, the snail either abandoned the prey, leaving behind an incomplete drill hole, or left no visible trace. In 53% of the attacks in the experimental table, snails abandoned their prey leaving no trace, while in the control table only 9% of attacks resulted in abandoned prey without any trace (Fig. 4.3 & 4.4). This difference is statistically significant (G = 91.4, p<<0.05, Likelihood-ratio test)

In the experimental table, the success rate of attacks depended on the presence of the crab and crushed conspecifics: in their presence, in 89% of cases (n = 63) the prey was abandoned; in their absence, abandonment occurred in 43% of cases (n = 30) (G = 21.2, p<<0.05, Likelihood-ratio test) (Fig. 4.5).

Impact on frequency of incomplete drill holes:

The frequency of incomplete drill holes in the experimental table (21.5%) was significantly higher than in the control table (1.1%; G = 23.6, p<<0.05, Likelihood-ratio test). Only one incompletely drilled mussel was recovered from the control table, and it was exceptionally big and thick (length = 46.27mm, thickness =1.42mm; for the mussels in control table, mean length = 27.68 ± 7.17mm and mean thickness = 0.66 ± 0.22mm). In the experimental table, two shells with one complete and one incomplete drill hole were found (Fig. 4.6a). In each instance a single snail produced both holes and was observed to relocate when the crab was introduced; presumably, the incomplete hole was produced initially, prior to disturbance and the complete hole subsequently. This suggests that these snails lack the ability to reoccupy the same spot when perturbed (c.f. Kelley and Hansen, 2003).

In the control table, one mussel had two complete drill holes, one on each valve (Fig. 4.6b). Two separate individuals were observed attacking this mussel and drilling simultaneously.

Time and/or size dependence of the incomplete drill holes:

The median size of mussels with incomplete drill holes is 26.08 mm whereas the median size of completely drilled mussels is 28.63 mm, but this difference is not statistically significant ($W = 222$, $p = 0.52$, Wilcoxon rank test). The lack of statistical significance might suggest that there is nothing of interest in this result, but this is not the case. The statistical test assumes that the median sizes of completely and incompletely drilled mussels should be the same (Ho: $\text{median}_{\text{complete}} = \text{median}_{\text{incomplete}}$), whereas one ought to expect them to differ: the median size of incompletely drilled mussels should be larger than of completely drilled mussels because smaller mussels have thinner shells and are presumably easier to handle, and on average it should take less time to drill a complete hole in a smaller mussel (Ho: $\text{median}_{\text{complete}} < \text{median}_{\text{incomplete}}$).The observed pattern is qualitatively opposite to this prediction, but to assess it quantitatively, a computer simulation was developed.

The variables used in the simulation were chosen such that the number and size of mussels and the number of complete and incomplete drill holes were similar to those in the actual experiments. In the computer simulation, 45 mussels were “attacked” and occupied by snails instantaneously at time $t = 0$. The drilling rate was obtained from regressing drilling time on mussel size for individuals that had been drilled to completion in the experimental table (Fig.4.7).

At each time increment, each snail could continue drilling its prey, consume its prey if it had penetrated the shell (complete drill hole), or abandon its prey with a probability, Pr (abandon). The probability of abandoning the prey was held constant in each time increment; it was calculated based on the observed proportions of incomplete (20/45) mussels in the experimental table. In each time increment, a tally was kept of mussels that had been penetrated and these were placed in a category "completely drilled"; abandoned mussels could not be re-occupied and were placed into a category "incompletely drilled." Each simulation was run for 200 time increments, equivalent to 200 hours. Given those parameters, at the end of each simulation approximately 20 mussels were incompletely drilled while 25 had complete drill holes, just as in the actual experimental observations. The distributions of sizes in each of the two categories as well as the median of each distribution were determined (Fig. 4.8). A metric, MEDDIF, the difference in median size between "completely drilled" and "incompletely drilled" was calculated; by repeating the simulation 1000 times, a frequency distribution of the MEDDIF metric was obtained.

As the simulation results illustrate (Fig. 4.9), the mode of the frequency distribution of MEDDIF, the differences in median sizes of completely and incompletely drilled mussels, is negative (-2.3 mm), in other words, the median size of completely drilled mussels is smaller than of incompletely drilled mussels. These results are in contrast to the experimentally observed difference in median sizes of complete and incomplete mussels which was positive (2.5 mm). A comparison between the observed difference to the results of the simulation, indicates that the two are significantly different at $p << 0.05$ (in more than 950 simulations, the difference in median size was smaller than the observed difference in medians size). This confirms our qualitative predictions and indicates that the observed differences in median sizes of completely and incompletely drilled mussels are significantly different from the null expectation, perhaps implying something about the behavior of snails.

What other mechanism could explain the slightly larger median size of completely drilled mussels? One possibility is that snails do not abandon their prey with constant probability when disturbed. For example, if a snail had already invested significant time, and thus energy, into drilling its prey, it would be less likely to abandon the prey when disturbed, than if it had invested little time into drilling its prey. Because it takes more time to penetrate a larger, thicker mussel, on average a snail occupying a larger mussel has occupied it longer than a snail occupying a smaller mussel and, if the probability of abandoning the prey decreases as a function of time of occupation, smaller prey would be more likely to be abandoned. Thus larger prey would be preferentially drilled to completion. The same pattern would result if snails somehow recognized the size of their prey and were less likely to abandon larger than smaller prey. Henceforth, the former scenario will be referred to as "time dependent" and the latter as "size dependent".

To explore the "time dependent" and "size dependent" scenarios described above, the computer simulations used previously were modified by adjusting the probability of abandoning prey, Pr (abandon). In the time dependent scenario, the snail's tenacity increases with time, i.e., the probability of abandonment drops with time. This was simulated by decreasing the probability of abandonment in each of time increments by a factor of 20/t, where t, time, ranges from 1 to 200. The results of 1000 simulations are summarized by the solid line in the same figure (Fig. 4.10). Note that the distribution has now shifted towards an increase in median size of the complete drill holes, and thus a decrease in the median size of the incomplete drill holes. Although the mode of this distribution is around 0, the experimentally observed difference of 2.5 is not statistically distinguishable from the distribution.

Finally, the simulation approach was used to evaluate the size dependence scenario. In this case, the probability of abandonment was time independent but varied as a function of the size of the prey (mussel), such that Pr (abandon) was proportional to the reciprocal of size (1/size), in other words, snails held onto larger mussels with greater tenacity. Fig. 4.11 illustrates the results of 1000 simulations. Again, the dashed line represents results of the null model (time and size independence) whereas the solid line, results of the size dependent model. The latter shows a shift in the distribution of the difference in the median sizes of completely drilled and incompletely drilled mussels towards the experimentally observed value of 2.5.

The simulations confirm that the experimentally observed sizes of completely and incompletely drilled mussels are indicative of snails possessing a complex predatory behavior. This behavior might be influenced by the size of their prey or by the time they have already invested into obtaining a meal. Neither the results nor the simulations allow to discriminate between these options, but these hypotheses are testable with future experiments or observations.

Discussion

In reconstructing the record of drilling predation from fossils, paleontologists commonly rely on data on drilling frequencies. Although different techniques exist for calculating predation intensity using drilling frequency data (Kelley & Hansen, 2003), the basic assumption is that drilling frequency is an indicator of the relative performance of predator and prey, performance that is a reflection of their intrinsic properties. But as this study clearly shows, extrinsic ecological factors might be extremely important in affecting drilling frequencies. In this study, the drilling frequencies were significantly lower in the presence of a secondary predator (24% vs 66%), in spite of the fact that the intrinsic properties of the predators and prey remained constant.

While in any given situation it might be difficult to evaluate the magnitude of the impact of secondary predators on drilling frequencies, this study suggests that when evidence of the presence of such secondary predators, either direct or indirect (shell breakage caused by crab claws, for example), exists, the recorded drilling frequencies might be lower than they would have been otherwise.

As for incomplete drill holes, these have been widely used to estimate the frequency of unsuccessful predatory events, both in recent (Vermeij *et al.,* 1989; Dietl, 2000) and fossil faunas (Vermeij, 1987, 2002; Kowalewski, 2002; Kelley & Hansen, 2003, 2006). The observations by Kowalewski (2004) on muricids, suggest that incomplete drill holes may overestimate the frequency of failed attacks because in some instances incompletely drilled prey were, in fact, killed. However, as this study demonstrates, incomplete drill hole frequencies might sometimes underestimate unsuccessful predatory attacks since an incomplete hole was produced in only 29% of the failed attacks in the experimental table; in 71% of cases, failed attacks left no mark on the prey.

The frequency of incomplete drill holes has often been used as an indicator of "prey-effectiveness" which is defined as the ratio of incomplete to attempted drill holes (complete + incomplete) (Vermeij, 1987). Increase in the frequency of incomplete drill holes has been interpreted as evidence of effective resistance against drilling predation. The metric of prey-effectiveness has also been used to document the dynamics of the escalation between drillers and their victims (In Vermeij, 1987, p. 311). Using this metric with data from the present study would suggest a 22-fold difference in "prey-effectiveness" between the control (1% of total attack) and experimental (22% of total attack) tables, but given that the prey and drilling predators in both sea tables came from the same populations, the difference is not a measure of adaptive differences in resistance against drilling predators, but rather a consequence of the presence of a secondary predator. It also represents an example of one of the two main emergent effects that is risk reduction caused by predator-predator interaction (Sih et al, 1998).

The incomplete drill hole data clearly suggest more complex behavior by predatory snails than simple abandonment of prey when a secondary predator is introduced. As shown through simulations, in the presence of a secondary predator the decision by the snail to either abandon or continue drilling its prey might be "time-dependent" or "size-dependent". Although it is difficult to distinguish between these two scenarios, the "size-dependent" scenario assumes that the snail has the ability to assess the size of its prey. Since such an ability should also be expressed by the snail while foraging, snails should select their prey based on size ("optimum foraging strategy", Krebs, 1977). If there is no appreciable size difference between attacked and non-attacked prey, "size dependence" can be eliminated as a plausible scenario. Unfortunately, the methods employed in this study do not allow for a test of such size selectivity.

Other results of this study with potential impact on the use of drill hole frequency data for estimating predation intensity relate to facultative predatory behavior. In this study, 13% of the prey were killed by *Nucella lamellosa* without drilling in the experimental table and only 2% in the control table, although the differences are not statistically significant. Such facultative predatory behavior has been observed among many drilling predators including naticids (Vermeij, 1980; Ansell & Morton, 1987; Kabat, 1990; Kelley & Hansen, 2003), octopods (Steer & Semmens, 2003) and muricids (Taylor *et al.*, 1980; Kent, 1981; Moran, 1985; Gutiérrez & Gallardo, 1999; Vermeij & Carlson, 2000); in some instances, more than 10% of the prey were killed without drilling (Vermeij, 1980). The exact cause of death of the prey in these examples is unclear. In some instances it has been suggested that it may represent unsuccessful attempts to drill (Kowalewski, 2004). For example, in aquarium experiments, Ansell & Morton (1987) observed the naticid *Glossaulas didyma* consuming some of its prey without drilling a complete hole; apparently, prey were suffocated during initial phases of drilling. In the present study, however, the lack of associated incomplete drill holes makes it difficult to assess whether drilling was even attempted. Perhaps death resulted from prey having experienced prolonged contact with the attacker (e.g. prey anesthesia by secretions from the hypobranchial gland; Moran, 1985; Taylor & Morton, 1996). Regardless of the exact cause of death or nature of predatory behavior, the killing of prey by drilling predators *without* drilling may be a relatively frequent phenomenon (Vermeij & Carlson, 2000), suggesting that drill hole frequencies might often be an underestimate of the intensity of interactions between drilling predators and their prey.

Conclusions

Drill holes in the shells of invertebrates represent one of the most unambiguous signatures of predator-prey interactions and have been commonly used by neontologists and paleontologists to explore ecological and evolutionary questions. While complete holes are by far the more common, frequency of incomplete holes is also informative and has often been invoked as a proxy for prey-effectiveness. Incomplete holes may be produced in several ways; here the impact of a secondary predator on incomplete drilling was investigated experimentally. Using the drilling muricid, *Nucella lamellosa* (Gmelin 1791) and its prey, the mussel *Mytilus trossulus* (Gould 1850), the frequency of incomplete holes was compared under two conditions: (1) when the gastropod’s natural predator, the crab *Cancer gracilis,* was present and (2) when it was absent. The presence of a secondary predator affected drilling activity, resulting in a significant increase in the frequency of incomplete drill holes. In the presence of a secondary predator, the overall drilling frequency also decreased. The decision by the gastropod to either abandon or continue drilling its prey when a secondary predator is present might be influenced by how much time it has already invested into drilling its prey, as shown by computer simulations. These results might have important consequences for the ecological and evolutionary implications of incomplete drill holes frequencies, for example, for their use in evaluating the evolutionary improvement of prey. Our future research will be directed to evaluating these effects using data from the Recent and fossil record.

	Events	Control sea table	Experimental sea table	
			Crab present	Crab absent
Successful attack	Drilled (complete)	78	5	16
	Undrilled (dead)	1	0	0
	Abandoned (dead)	0	2	1
Failed attack	Incompletely drilled	1	18	2
	Abandoned (alive)	8	38	11

Table 4.1: Table summarizing all the results of predatory attacks in two sea tables.

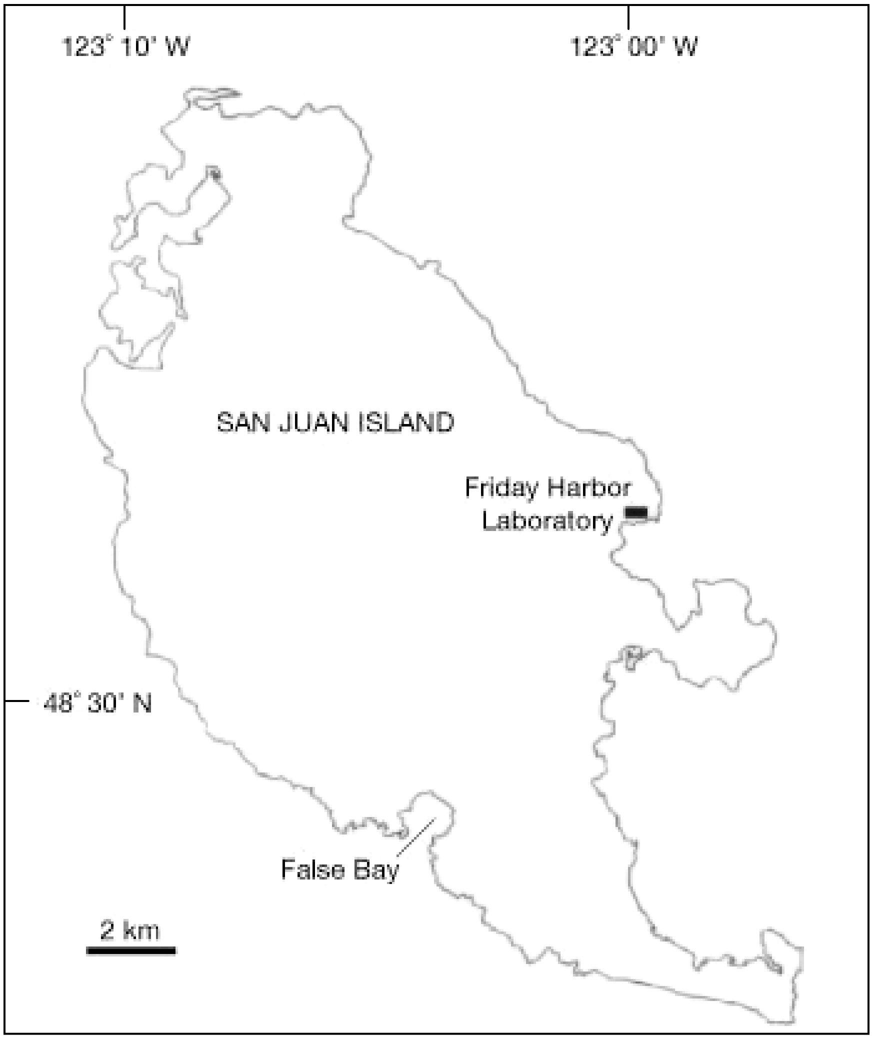

Figure 4.1: Location map of False Bay in San Juan Island, WA, USA.

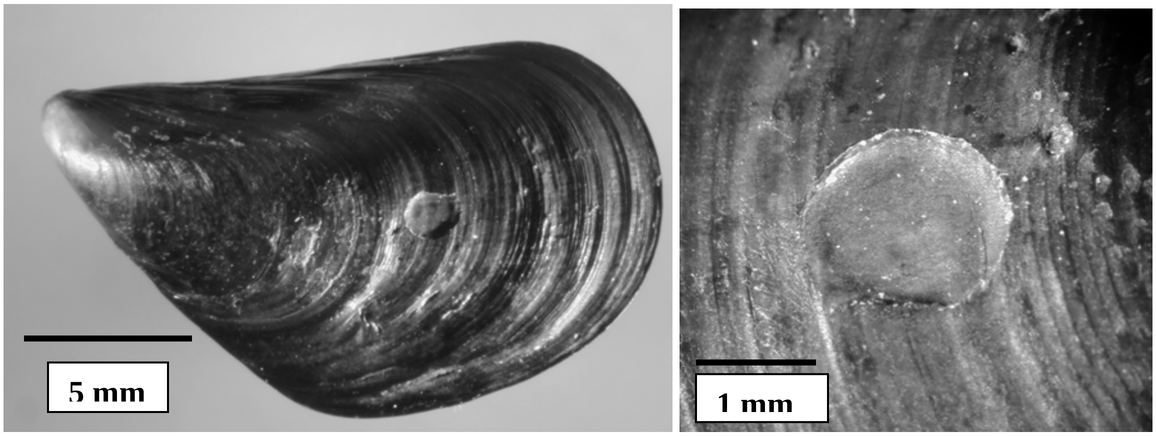

Figure 4.2: In the left, a shell of *Mytilus trossulus* with incomplete drill hole produced by *Nucella lamellosa* in the experimental sea table. In the right, a close up view of the incomplete drillhole.

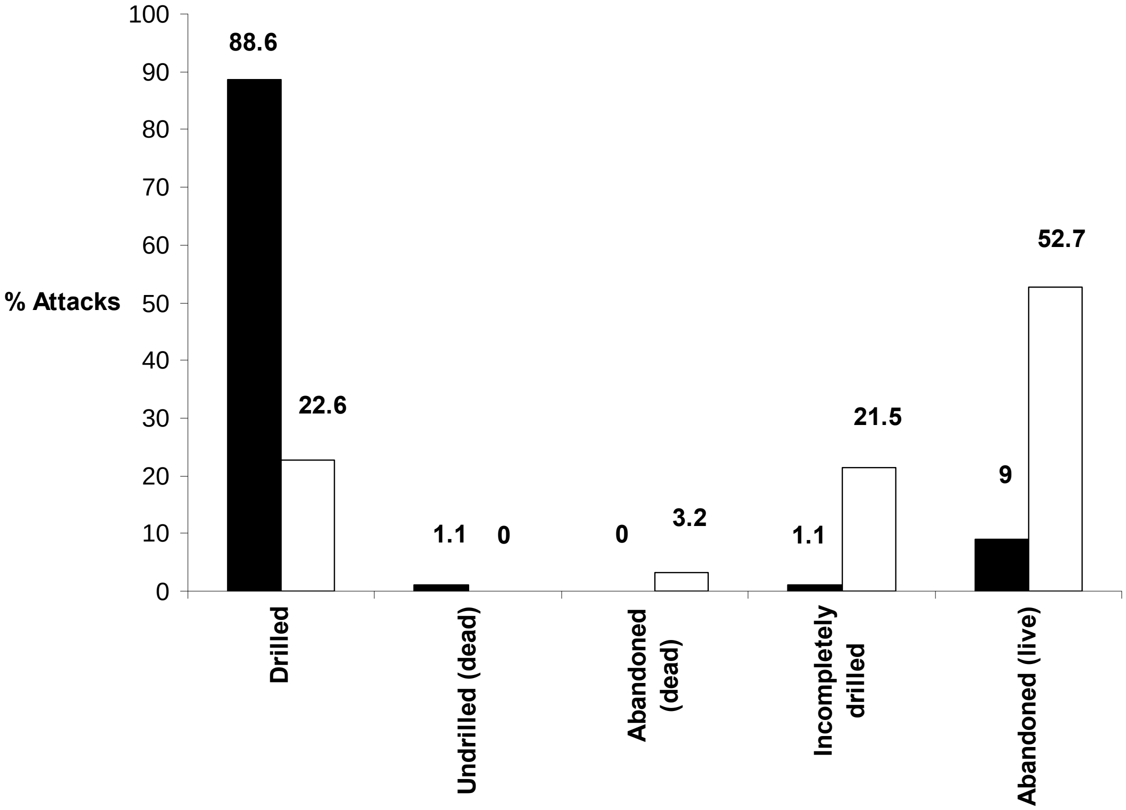

Figure 4.3: Frequency of different results of attacks in two sea tables by the drilling predator *Nucella lamellosa*. Results are presented up to one decimal place. The black bar represents the control sea table and the white bar represents experimental sea table.

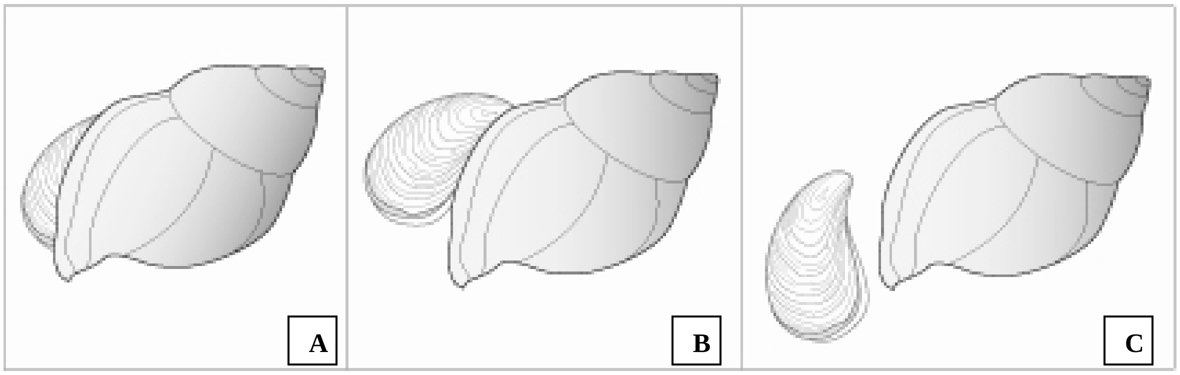

Figure 4.4: Sketch showing the sequence of abandoning a prey. Time elapsed between A and C is approximately 15 minutes. In this case the snail did not leave any predation mark on the mussel.

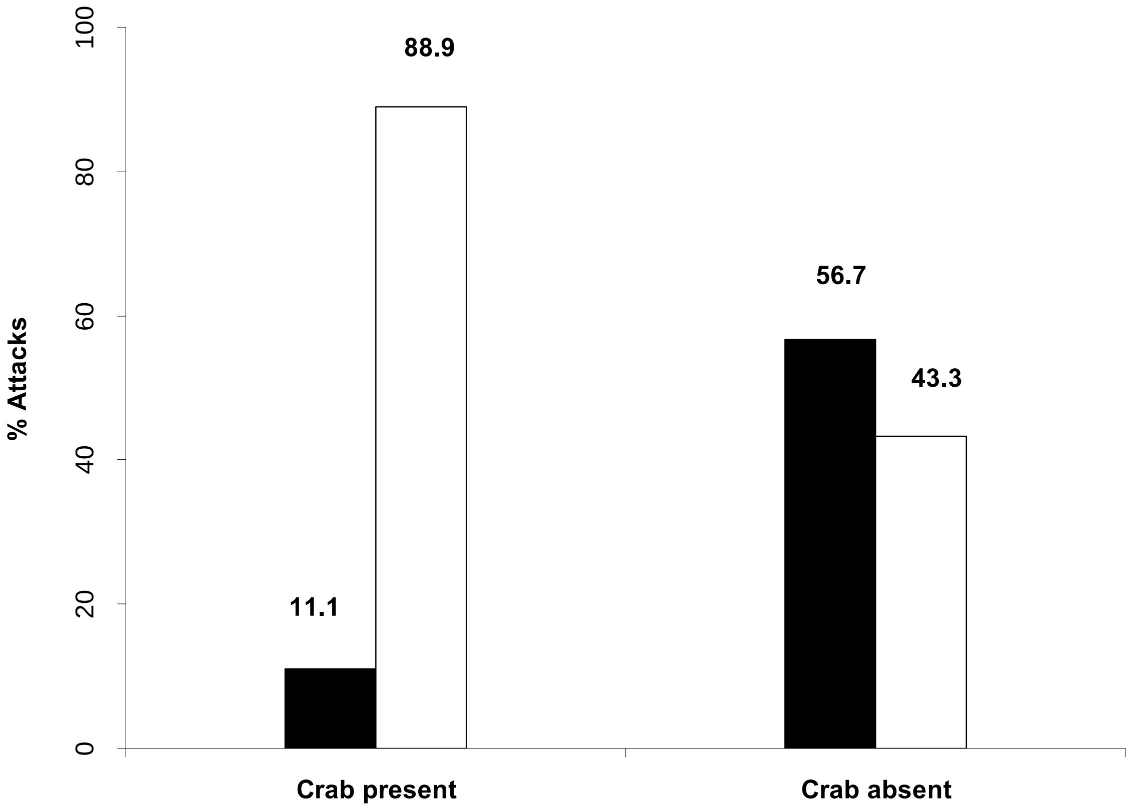

Figure 4.5: Frequency of abandoned and successful attacks in the presence and absence of the crab in the experimental sea table. Black bar represents successful attack and the white bar represents failed attack. Results are presented up to one decimal place. When the crab is absent in the experimental table, the frequency of successful attacks increases and the instances of abandonment decreases. The scenario gets completely reversed with the presence of the crab.

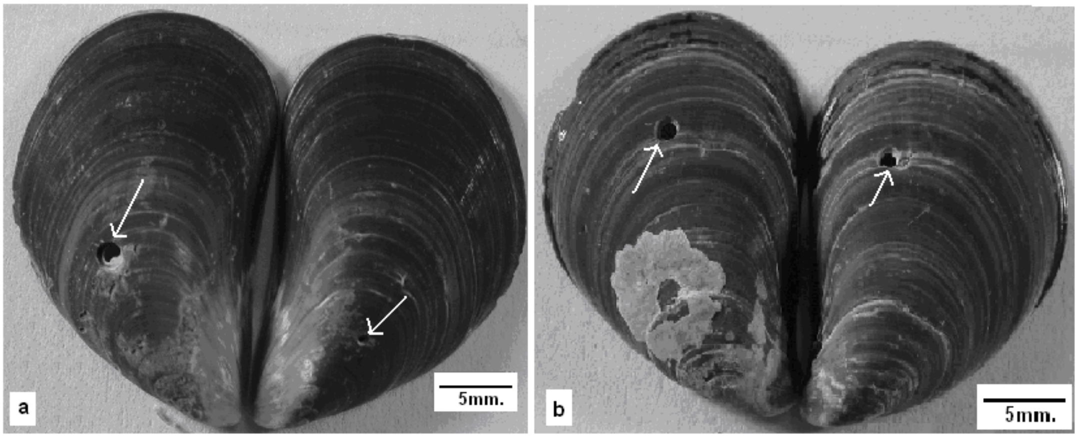

Figure 4.6: a. *Mytilus trossulus* with one complete and one incomplete drill hole. Both the drill holes were made by one *Nucella lamellosa* individual. b. One *Mytilus trossulus* individual with two complete drill holes on both valves. It has been drilled by two *Nucella lamellosa* simultaneously.

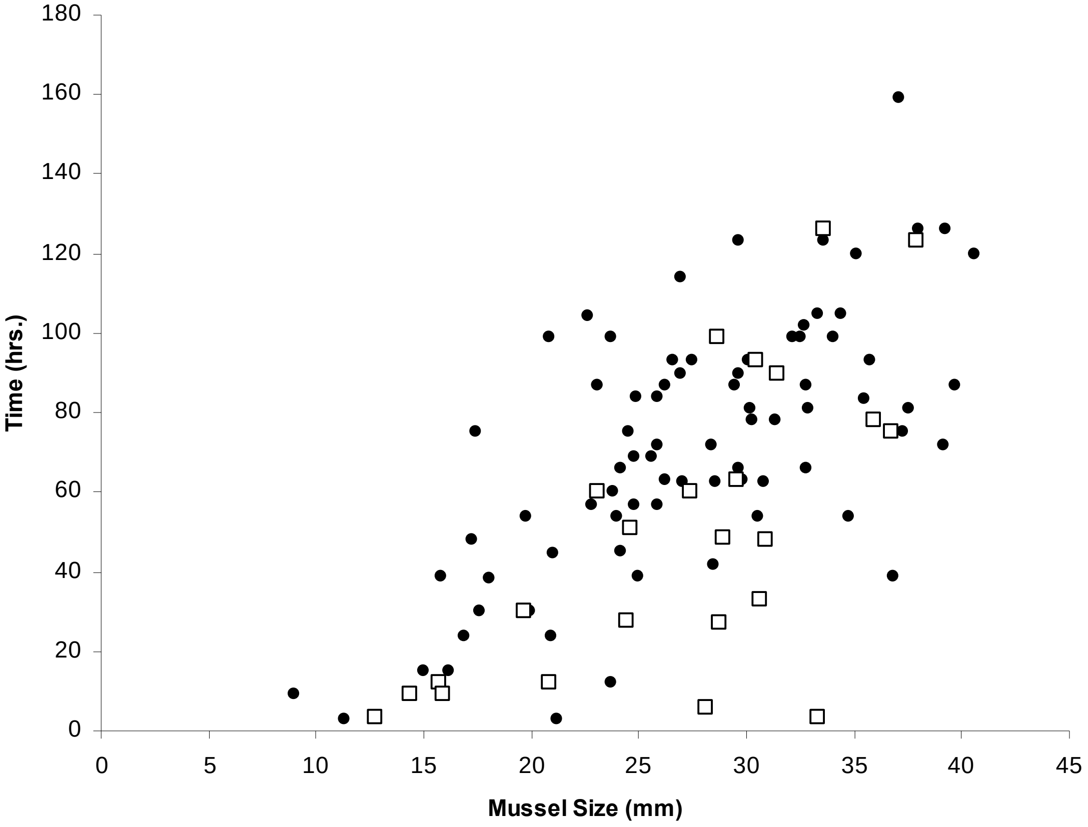

Figure 4.7: Plot showing the relationship between length of the mussel and the drilling time. Solid circles represent control sea table and the open squares represent experimental sea table.

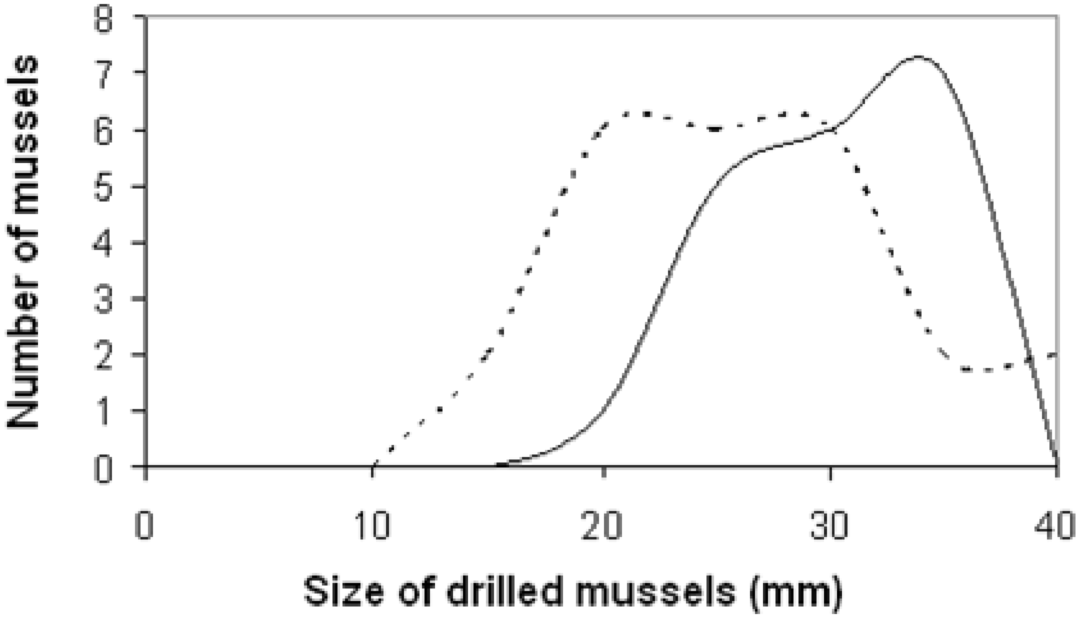

Figure 4.8: Result of a single run of unbiased (random) drilling and abandonment. Solid line represents incomplete drill holes (median = 29.5 mm) and dashed line represents complete drill holes (median = 24.4 mm).

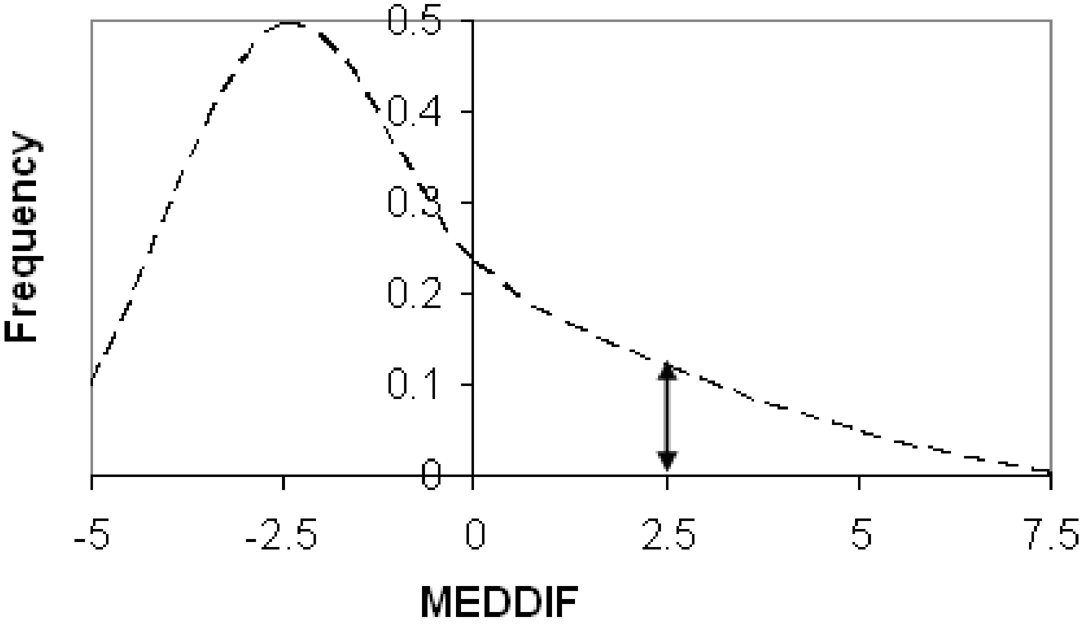

Figure 4.9: Results of the simulation for the null model. The double pointed arrow is plotted at a value of the observed difference in median sizes of complete and incomplete mussels.

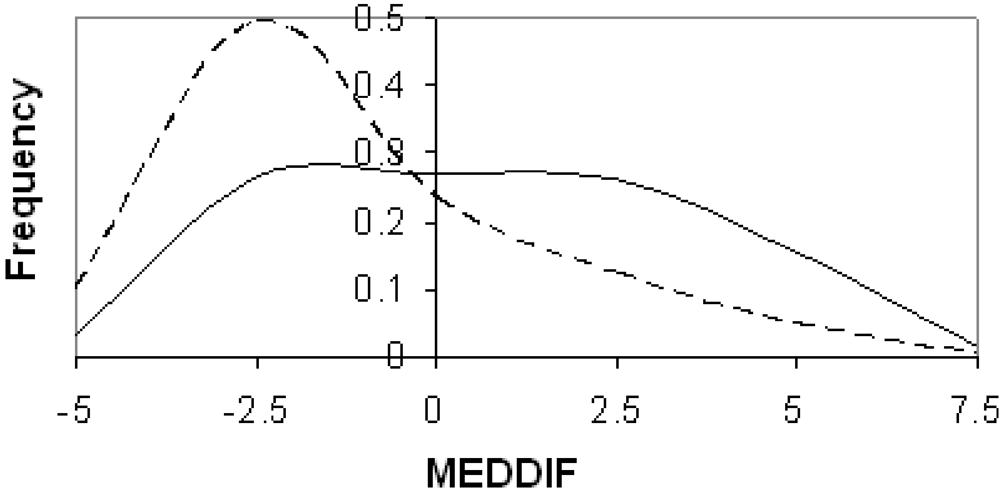

Figure 4.10: Results of the simulation for time-dependant model. The solid line represents a scenario with Pr (abandon) proportional to 20/time where as the dashed line is the result of simulation of time independent model (null model).

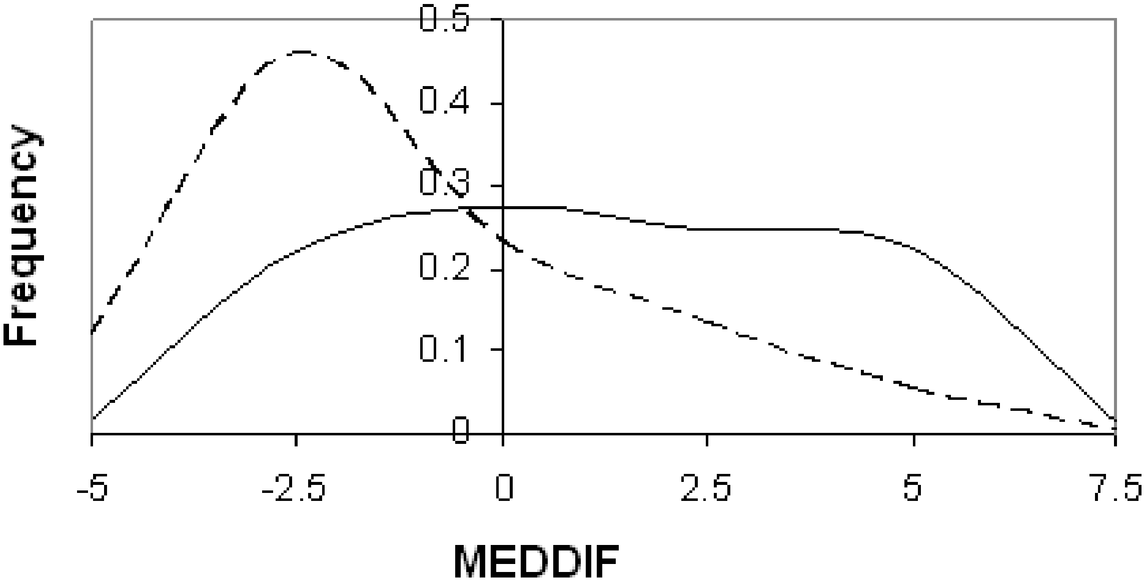

Figure 4.11: Results of the simulation for size-dependant model. The dashed line represents the result of the simulation for the null model. The solid line represents a scenario with Pr (abandon) proportional to 1/size where as the dashed line is the result of simulation of size independent model (null model).

CHAPTER 5

EFFECT OF DUROPHAGY ON DRILLING PREDATION: A CASE STUDY OF CENOZOIC MOLLUSCS FROM NORTH AMERICA

Introduction

Predator-prey interactions have been a topic of interest to paleontologists due to their ecological importance but especially because of their potential evolutionary implications. For example, predation has been claimed to influence rates of evolution (Stanley, 1974), considered a causal factor in the rise of biomineralization (Stanley, 1976; Conway Morris and Bengston, 1998) and in diversification and extinction (Vermeij, 1987; Jablonski and Sepkoski, 1996). Also, it has been suggested that predator-prey interactions drive long-term morphological and behavioral trends in various clades (Signor and Brett, 1984; Vermeij, 1987) and finally two important concepts assume predation to be a major agent of evolutionary change--coevolution and escalation.

One of the main problems in testing evolutionary hypotheses that emphasize predation such as the ones listed above, is that direct evidence of most predator-prey interactions is rare or absent in the fossil record (Leighton, 2002). While the absence of direct evidence is not fatal to such hypotheses, it does make them difficult to test; therefore identifying predator-prey systems for which such evidence is available is highly desirable. Predation by drilling gastropods on their shelled, typically molluscan, prey represents one such system. Drilling gastropods often leave distinct markings on their shelled prey making it possible not only to identify the victims but also the predators and, importantly, to obtain quantitative estimates for a variety of relevant metrics. Such metrics include the frequency of drill holes, used to estimate predation intensity (Taylor, 1970; Stanton and Nelson, 1980; Vermeij et al., 1980; Vermeij and Dudley, 1982; Kabat and Kohn, 1986), frequencies of incomplete drill holes used as a measure of failed predation events (but see Kowalewski, 2004) and thus prey-effectiveness (Kelley and Hansen, 2001), position of drill holes and distribution of sizes of prey used to evaluate predatory strategies, and taxonomic distribution of drill holes used to explore selectivity. The drilling predator-prey system, because it is common in modern marine environments, also has the advantage of providing researchers an opportunity for studying its details through neontological experiments. As a consequence, drilling predator-prey systems have drawn a lot of attention over the past couple of decades (summarized by Kowalewski *et al.*, 1998). Some of these studies have used drilling frequencies to test different hypotheses about prey-selectivity (Ausich and Gurrola, 1979; Vermeij and Dudley, 1982; Hoffman and Martinell, 1984; Colbath, 1985; Tull and Bohning-Gaese, 1993; Leighton, 2003), predator behavior (Berg and Nishenko, 1975; Zlotnik, 2001; Deline *et al.*, 2003) while others have explored broad scale temporal patterns in predation intensity based on drilling frequency data (Vermeij, 1987; Kelley and Hansen, 1993; Kowalewski *et al.*, 1998; Huntley and Kowalewski, 2007).

Another type of predator–prey interaction that offers similar advantages is duropophagy, since shell-crushing predators sometime leave diagnostic marks on their prey. Although two categories of pre-ingestive breakage have been recognized, namely lethal and sublethal (repaired) damage, lethal fractures are often less diagnostic of the causal agent and are often indistinguishable from abiotic (taphonomic) agents of shell degradation; sublethal damage, on the other hand, is relatively easy to identify. Consequently, repair scar frequencies are more commonly used in studies of durophagous predation. For example, they have been used to evaluate the importance of predation as a selective agent (Andrews 1935; Rand, 1954; Vermeij *et al.*, 1981; Vermeij 1982; Allmon *et al.*, 1990; Huntley and Kowalewski, 2007). Although it must be recognized that repair scars represent failed attacks and are thus analogous to incomplete rather than complete drill holes (Vermeij, 1987; Allmon *et al.*, 1990; Leighton, 2001, 2002; Harper, 2006), they can be used as proxy for predatory activity. This is supported by a recent study with live blue crabs and periwinkles by Moody and Aronson (2007) which demonstrated that the occurrence of sublethal shell repair in *Littorina* was positively correlated to the frequency of predatory attacks and the abundance of crabs.

In most paleontological studies of predator-prey interactions, the system has been treated from a two-taxon perspective, that of the predator and its prey; interactions with other predators have generally not been considered. However, among ecologists the past few decades have seen much discussion devoted to the interaction between different predator groups and the resulting "emergent effects" (Sih *et al.*, 1985, 1998; Lima and Dill, 1990). Given that natural communities typically have multiple predators feeding on many prey, understanding emergent multiple predator effects (MPEs) is a critical issue for community ecology (Wilbur and Fauth, 1990; Wooton, 1994). Studies suggest two main types of emergent effects–1) risk reduction caused by predator–predator interactions and 2) risk enhancement caused by conflicting prey responses to multiple predators. However, very few studies have been designed to test for coevolution and escalation in the context of MPEs (Dietl and Kelley, 2004). For studies of drilling predation, which are often used in testing temporal trends, MPEs may be especially important as they have the potential for affecting drilling frequencies and thus affecting conclusions based on drilling frequency data.

Influence of durophages on drilling predators:

A number of recent studies have looked into the behavioral response of prey in the presence of a predator. Some of these studies have emphasized trait-mediated indirect interactions (TMII) (Abrams *et al.*, 1996). For example, waterborne cues ("risk cues") released by predators can cause changes in prey species behavior, such as feeding rates, thereby altering the impact of the prey species on their resources. Thus, TMIIs represent the nonlethal effects of predators that contrast with the more traditional emphasis on lethal indirect effects.

Predator-induced changes in prey behavior that reduce risk of predation, such as alterations in feeding rate or habitat use (Dill 1987; Lima 1988*a*, *b*; Werner and Anholt 1993; Turner 1996; Turner *et al.*, 1999) also may modify the prey's impact on its resources (Turner and Mittlebach 1990; Turner 1997; Turner *et al.*, 2000). For instance, snails exposed to predatory crabs exhibit reduced activity, reduced feeding levels, and increased use of inconspicuous or ''refuge'' habitats (Palmer 1990; Marko and Palmer 1991). Palmer (1990) noted that *Nucella lapillus* feeding in the presence of green crab preferred to consume barnacles located on the underside rather than on top of stones placed within experimental chambers. In contrast, *N. lapillus* feeding in the absence of these cues showed little discrimination with respect to the position of their barnacle prey and consumed significantly more barnacles.

Trussel *et al.* (2003) examined whether risk cues released by a secondary predator (blue crab) influenced the behavior of its snail prey and whether this was reflected in the abundance of the snail's two dominant prey species, barnacles and fucoid algae. They found that the presence of crab risk cues had strong cascading indirect effects on the abundance of barnacles and fucoid algae. Gastropods exposed to risk cues consumed significantly fewer barnacles and algae compared to conspecifics feeding in the absence of risk cues. The snails also exhibited more refuge-seeking behavior and grew less in the presence of risk cues.

In another recent experimental study (Chattopadhyay and Baumiller, 2007), the presence of a secondary predator (a crab) was found to have a significant effect on the behavior of a drilling predator (muricid gastropod) preying upon mussels: in the presence of the crab the driller's success rate decreased resulting in a decrease in overall drilling frequency and an increase in incomplete drilling frequency (increase in prey-effectiveness).

The above neontological studies suggest that the mere presence of a secondary predator may have a significant effect on the predator and this is likely to have been the case in natural systems of the past. To test this in the fossil record requires being able to measure the activity of secondary predators as well as those of drilling predators. In this study, using repair scar as a proxy for the activities of durophagous predators (which are most commonly the secondary predators), we test the affected behavior of drilling predators, as measured by the frequencies of complete and incomplete drill holes.

Materials and methods

The Plio-Plesitocene geological record of North America contains numerous localities in which drilling snails and their molluscan prey (both bivalves and gastropods) are common. Specimens from these localities show evidence of frequent, though variable, predatory activities of these snails as evidenced by drill holes. While fossils of durophagous predators are much less common, their activities are preserved in the form of repair scars. Using collections from six Plio-Pleistocene localities in Florida, North Carolina and California housed in the Museum of Paleontology, University of Michigan, we examined 18,963 fossil specimens of 18 bivalve genera and 14 gastropod genera for evidence of durophagous and drilling predation (Table. 5.1). The number of specimens from each locality ranged from 300-7000 and three to six genera. For each locality each species was represented by at least 20 individuals. Specimens were sorted based on the presence of predation marks such as complete drill holes, incomplete drill holes, and repair scars (Fig.5.1A-F). Drill hole morphology was categorized either as counter-sunk or cylindrical as it provides some clues about the identity of the predator (Kelley and Hansen, 2003). The specimens were manually counted after sorting.

Three parameters were calculated: repair scar frequency, drilling frequency and incomplete drill hole frequency. For gastropods, the drilling frequency was calculated by dividing the number of complete drill holes by the total number of individuals. In calculating repair scar frequency, we adopted the "scars per shell" method (Vermeij *et al.*, 1981; Dietl and Alexander, 1998; Dietl *et al.*, 2000; Alexander and Dietl, 2001) where the total number of repair scars was divided by the total number of individuals in a sample. Since all of our bivalve specimens were disarticulated, we used the formulae recommended by Kowalewski (2002) dividing the number of individuals with predation marks by half the total number of valves. The formula for incomplete drill hole frequency is the same for bivalves and gastropods since it is not affected by disarticulation and it was calculated by dividing the number of incomplete drill holes by the sum of complete and incomplete drill holes (it is the same formulae used to calculate prey-effectiveness defined by Vermeij, 1987). Initially average drilling frequency, repair scar frequency and incomplete drilling frequencies were calculated for each species present in each of the six localities. Using these averages, the average value of the three parameters (drilling, repair scar, incomplete drilling) was calculated for each locality. Average drilling frequency, repair scar frequency and incomplete drilling frequency for each locality were also calculated for bivalves and gastropods separately.

In order to obtain average length and thickness, we also measured the length and thickness of 25 random individuals from each species using digital calipers (to the nearest

0.01mm). We measured thickness at a fixed point in the midsection of the bivalve shells. For the gastropods, thickness was measured near the aperture. Average thickness of the shell for each locality was calculated separately for bivalves and gastropods.

Results

A significant negative relationship exists between average repair scar and drilling frequencies for both bivalves (Spearman $\rho = -0.81$, $p = 0.03$) and gastropods (Spearman $\rho = -0.94$, $p <= 0.01$) (Fig.5.2 and 5.3). Levels of significance were obtained using a bootstrap technique (see appendix). When bivalves and gastropods are considered together, there is a significant negative relationship between overall drilling and repair scar frequencies (Chi-square test, $p = 0.02$) (Fig.5.4 and Table.5.2).

A significant positive relationship exists between repair scar and incomplete drill hole frequencies for bivalves (Spearman $\rho = 0.91$, $p = 0.02$) (Fig. 5.5). The same holds true for gastropods, although it is marginally significant (Spearman $\rho = 0.54$, $p = 0.05$) (Fig. 5.6). When bivalves and gastropods are considered together, there is a marginally significant positive relationship between incomplete drilling and repair scar frequencies (Chi-square test, $p = 0.05$) (Fig.5.7 and Table.5.3).

Discussion

In this study, we asked whether frequencies of complete and incomplete drill holes might be correlated with frequencies of repair scars, testing the hypothesis that the behavior of drilling predators is significantly impacted by the activities of secondary, durophagous predators. The results are consistent with this prediction: the frequency of complete drill holes is significant and negatively correlated with repair scars frequencies, whereas a significant, positive relationship characterizes frequencies of incomplete drill holes and repair scars. Before discussing the implications of these results in the context of our hypothesis, we first explore other ways in which the observed pattern might have been generated. It is essential to recognize that some factors (for instance, abundance of predator, taphonomic artifacts), although important in changing the frequencies separately, are most unlikely to generate such a pattern

Shell Thickness:

Shell thickness is generally thought to be an important anti-predatory strategy (Vermeij, 1983; Roopnarine and Beussink, 1999; Dietl *et al.*, 2000; Alexander and Dietl, 2003; Leighton, 2003) and differences in shell thickness of specimens found at different localities could generate a correlation similar to the observed patterns. For example, increasing shell thickness should lead to a decrease in drilling frequencies while incomplete drill hole frequencies should increase. Thicker shells should also be more resistant to durophagous predation and this should lead to an increase in the incidence of unsuccessful attacks (repair scars). Hence, it is possible that varying thickness could produce a negative correlation between repair scar and drilling frequency, and a positive correlation between repair scar and incomplete drill hole frequency.

However, in our samples, we found no significant trends in complete drill hole, incomplete drill hole, and repair scar frequencies with thickness and we can reject this hypothesis. In fact, the trends we found were opposite to those predicted by the "shell thickness" scenario (Fig. 5.8-5.10): the frequency of complete drill holes increased, of incomplete drill holes and repair scars decreased with increasing shell thickness.

Prey Selectivity:

The taxonomic compositions of localities used in this study differ. Assuming that predators vary in their preferences, if prey taxa preferred by a drilling predator were found at one locality but only less preferred prey were found at another, differences in drilling frequencies might result regardless of secondary predators. Similarly, if the prey, although preferred by drilling predators, rank low on a durophage's menu, a negative correlation between drilling and durophagous predation intensity might result.

The above highly contrived scenarios are unlikely because taxa in our samples are generally known to be heavily preyed upon by both drilling and durophagous predators based on reports from other localities (Kitchell *et al.*, 1981; Anderson *et al.*, 1991; Roopnarine and Beussink, 1999; Alexander and Dietl, 2001), the number of taxa at any locality is relatively large and the same scenario would have to apply to all taxa, and, finally, neither of the scenarios would explain the pattern for incomplete drill holes.

Nevertheless, to test this hypothesis further, we restricted our analysis to a single taxon, *Neverita duplicata,* found in three of the six localities. For this single taxon, the relationship between drilling frequencies, incomplete frequencies and repair scar frequencies are the same as those for all bivalves and gastropods (Fig. 5.11 and 5.12).

Repair scars as proxy of durophage activity:

The frequency of repair scars is a commonly used proxy for durophagous predator activities. For example, it has been used to evaluate the importance of predation as a selective agent (Vermeij 1982). Repair scars have also been used for durophagous predator activity with altitude (Ballinger 1979; Shaffer 1978), with latitude (Schall and Pianka 1980), between islands and mainland (Rand 1954), and between freshwater to marine habitats (Andrews 1935). It has also been used to explore the relationship between predation intensity and global diversity (Huntley and Kowalewski, 2007). Nevertheless, because repair scars record failed attacks, their use as a measure of predator activity is not straightforward (Leighton, 2001). Under some scenarios, increase in repair frequency can be a consequence of increasing prey resistance rather than predatory activity. Can the latter possibility be excluded in this study?

If repair frequency correlates with prey resistance rather predator activity, one should be able to test this by examining repair frequencies as function of some morphological traits, such as shell thickness, that affect prey resistance. As our discussion of “shell thickness” above (Fig. 5.12) indicates, no significant trend exists between repair scar frequency and shell thickness. Moreover, if differences in repair scar frequencies were due to differences in prey resistance rather than in activities of secondary predators, a single prey species occurring across many localities, should exhibit near constant frequencies of repair scars (assuming its resistance is constant across localities). As discussed above (“prey selectivity”) *Neverita duplicata* shows a broad range of repair scar frequencies.

Latitude:

Predation intensity as function of latitude has been the subject of much research (Vermeij *et al.*, 1989; Allmon *et al.*, 1990; Hansen and Kelley, 1995; Hoffmeister and

Kowalewski, 2001; Dudley and Vermeij, 1978; Alexander and Dietl, 2001; Kelley *et al.*, 1997) and we must therefore consider the possibility that our repair scar and drilling frequency results might be a reflection of some unusual combination of latitudinal differences in predation activities rather than being causally connected.

The latitudinal effect for the observed patterns can be rejected because (1) the latitudinal range of our localities is very narrow (~10º), (2) there is no significant relationship between latitude and frequencies of drill holes and repair scars in our data (Fig. 5. 13 & 5.14), and (3) the variation in drill hole and repair scar frequencies among latitudinally more proximate localities is of the same magnitude as variation for localities that are far apart rather than being more similar for latitudinally more proximate localities.

Implications

In reconstructing the record of drilling predation from fossils, paleontologists commonly rely on drilling frequency data. For example, some studies have used such data to compare predation intensities between different areas during the same (or nearly the same) temporal span (Jonkers, 2000; Leighton, 2001; Walker, 2001; Baumiller and Bitner, 2004) while others have used them to analyze temporal trends in predation intensity (Sohl, 1969; Dudley and Vermeij, 1978; Taylor *et al.*, 1983; Allmon *et al.*, 1990; Hagadorn and Boyajian, 1997; Harper *et al.*, 1998; Dietl and Alexander, 2000; Leighton, 2003; Amano, 2006; Kelley and Hansen, 2006). Although it is recognized that such frequencies may be influenced by extrinsic factors, in general they are interpreted in the context of predator and prey only. However, as a number of neontological studies illustrate, natural systems might be multi-tiered and include secondary predators, and that can have a significant impact on drilling frequencies. In those instances, interpreting changes in frequencies as due to changes in the relative performance of drilling predators and their prey would be inaccurate.

In this study, the presence of secondary predators was recognized from repair marks made by shell-crushing predators, but pre-ingestive breakage or crushing is only one of four methods of molluscivory, the others being whole-organism ingestion, insertion and extraction, and drilling (Vermeij, 1987; Harper and Skelton, 1993).

Unfortunately, whole-organism ingestion, and insertion and extraction, although common, are unlikely to leave preservable evidence. As a consequence, the effect of these predators on drilling predation is likely to go unnoticed.

The complexities and outcomes of multi-tiered interactions prompt us to revisit concepts of coevolution and escalation. The major difference between coevolution and escalation is in the nature of selection (Vermeij, 1994). Escalation is enemy-driven evolution where the role of prey (with exception of dangerous prey) is relatively unimportant in arms races between predator and prey. In coevolution, prey are linked tightly to their predator and are thought to drive the predator's evolution. In the presence of secondary predators the predictions of these two hypotheses differ. If escalation is acting, one would expect changes in traits (morphological or behavioral) of the predator (such as the drilling gastropod) to be a function of its predator's (secondary predator) activity, whereas under a coevolutionary scenario, evolutionary change in the predator would be primarily in response to its prey. In the long run, if escalation is the prevalent mode of change, changes in drilling and incomplete drilling frequency would be a function of activity of secondary predators. However, in nature the evolutionary mode is likely to be a combination of the two. For instance, we might expect to see changes in behavioral traits such as drilling rate, feeding rate or stereotypy that would give some evolutionary advantage to the driller against the mortality risk imposed by the predator. These traits, however, would also be affected by the response of the prey. In order to evaluate the nature of evolutionary change in multi-tiered predator-prey systems, a proper assessment of risk through time is necessary. In cases such as represented by this study, the risk for a drilling predator through time is likely to be dependent on the diversity (and success) of durophagous predators. It has been recognized that the evolution and diversification of durophagous predators through the Phanerozoic had profound effects upon the structure of benthic communities (Bambach, 1993; Bottjer, 1985) and upon the evolution of shelled invertebrates. How much it affected the evolution of the behavior of drilling predators, is yet to be evaluated. A similar yet slightly different approach would be to evaluate the effect of disappearance of a durophagous group on drilling predation.

The impact of secondary predators may also be recognized in the Recent by comparing systems in which activities of durophages differ. For example, whereas durophagous predation remains strong in the Arctic (Dayton, 1990), it has been virtually absent from Antarctica from Eocene onwards (Aronson and Blake, 2001). One prediction of this pattern based on the results of this study is that higher drilling frequencies and lower incomplete drilling frequencies should characterize Antarctic assemblages compared to Arctic assemblages.

Conclusions

In reconstructing the record of drilling predation from fossils, paleontologists commonly rely on data on drilling frequencies. Temporal patterns in drilling frequencies have been used as evidence of arms race. Using Plio-Pleistocene fossil assemblages, we demonstrated that there is a strong negative relationship between repair-scar and drilling frequency which is consistent with our hypothesis of a deterrent effect of secondary predator on drilling predation. The observed positive relationship between repair scar and incomplete drilling frequency also supports our hypothesis. Although, drilling frequency has been used in the context of co-evolution and escalation, it has always been analyzed in the context of a two taxon system. Modern neontological literature demonstrates that often the effect of threat of an enemy modifies the behavioral response of a predator. Since frequency of complete and incomplete drill holes often depends on the driller's behavioral response to ambient threat, it could be used as an important proxy of behavioral response in tracking the mode of "enemy driven evolutionary change" or escalation through time.

Appendix

Although our specimen size is quite large (~1900), testing the patterns among 6 localities reduce the number of data points to only six. Consequently, a computer simulation using resampling was developed to test the null hypothesis of no correlation between repair scar- drilling frequency and repair scar frequency-prey-effectiveness (Ho: Spearman $\rho_{\text{repair scar-drilling}}$ = Spearman $\rho_{\text{repair scar-prey-effectiveness}} = 0$). Spearman ρ was used to measure the correlation between any two sets of variables. The simulation allowed us to ask how many times a trend comparable to the observed one could be produced by chance. We generated drilling frequency data for each locality by randomly choosing drilling frequencies from the list of observed drilling frequencies.

The same procedure was used to generate repair scar frequencies. Once simulated frequencies had been generated for all localities, the average repair scar frequency and drilling frequency could be calculated of for each locality. Spearman ρ was used as a measure of correlation between average repair scar frequencies and drilling frequencies. After each iteration, Spearman ρ was calculated by correlating the 6 data points on that run. By running the simulation1000 times, a frequency distribution of the “ρ”s was obtained and this was compared to the observed ρ (Fig. 5.15 and 5.16).The same approach was used to explore the relationship between repair scar frequency and incomplete drilling frequency (Fig.5. 17 and 5.18).

Locality	Taxa	Drilling frequency	Repair scar frequency	Incomplete drilling frequency
Neuse River, NC (James City Fm.)	*Tellina alternate*	6	35	67
	Spisula solidissima	23	23	50
	Donax sp.	9	9	45
	Nucula proxima	24	8	25
	Corbula contracta	12	18	67
	Trachycardium sp.	19	11	37
	Mulinia lateralis	9	16	59
	Noetia sp.	15	8	64
	Mulinia sp.	8	13	22
	Chione sp.	20	12	29
	Tellina sp.	6	17	0
	Anadara transversa	12	17	29
	Crepidula plana	35	20	30
	Cancellaria reticulate	19	6	27
	Terebra dislocate	35	0	25
	Oliva sayana	6	6	0
	Neverita duplicate	25	13	0
	Marginella sp.	6	6	0
Punta Gorda, FL (Caloosahatchee Fm.)	*Chione elevate*	94	4	6
	Tellina alternate	22	0	29
	Anadara transversa	13	1	24
	Eucrassatella speciosa	18	6	33
	Neverita sp.	17	37	0
Miami Canal, FL (Caloosahatchee Fm.)	*Chione elevate*	27	1	17
	Mulinia lateralis	9	4	0
	Arca sp.	6	0	67
	Natica plicatella	24	2	18
	Oliva sayana	50	2	8
	Neverita duplicate	20	12	19
	Strombus alatus	4	14	50
McQueen’s pit, FL (Caloosahatchee Fm.)	*Anadara transversa*	18	2	0
	Chione elevate	21	10	30
	Tellina sp.	62	3	8
	Eucrassatella speciosa	2	9	0
	Neverita duplicate	0	38	100
	Cerithium atratum	4	4	0
	Transennella tantilla	20	3	5
Deadman’s Island, CA (San Pedro Fm.)	*Phacoides californicus*	33	7	0
	Phacoides sp.	12	13	27
	Paphia staminae	46	2	1
	Amphisa versicolor	7	3	0
	Alectrion perpinguis	10	3	0
	Alectrion mendicus	12	5	0
	Alectrion ? mendicus	7	11	0
	Tricolia sp.	2	4	8
	Alia carinata	2	23	39
	Alection cooperi	3	24	0
	Lacuna compacta	2	10	0
	Alia sp.	1	22	0
	Alection ?cooperi	10	6	1
	Mitrella gausapata	2	20	29
	Mitrella sp.	5	26	29
	Alectrion sp.	6	9	0
	Ostrea virginica	13	97	0
Chiquita, FL (Caloosahatchee Fm.)	*Tellina alternate*	13	3	25
	Brachidontes sp.	3	83	67
	Chione elevate	4	30	46
	Marginella sp.	8	42	0
	Cerithium atratum	0	35	100
	Neverita duplicate	5	15	50

Table 5.1: List of bivalve and gastropod species from six localities used in this study.

	Drilling frequency →	
Repair scar frequency ↓	10	20
	18	13

Table 5.2: Contingency table for the Chi-square test performed to evaluate the correlation between drilling frequency and repair scar frequency of bivalve and gastropods.

	Incomplete drilling frequency	
Repair scar frequency	19	11
	11	20

Table 5.3: Contingency table for the Chi-square test performed to evaluate the correlation between repair scar frequency and incomplete drilling frequency of bivalve and gastropods.

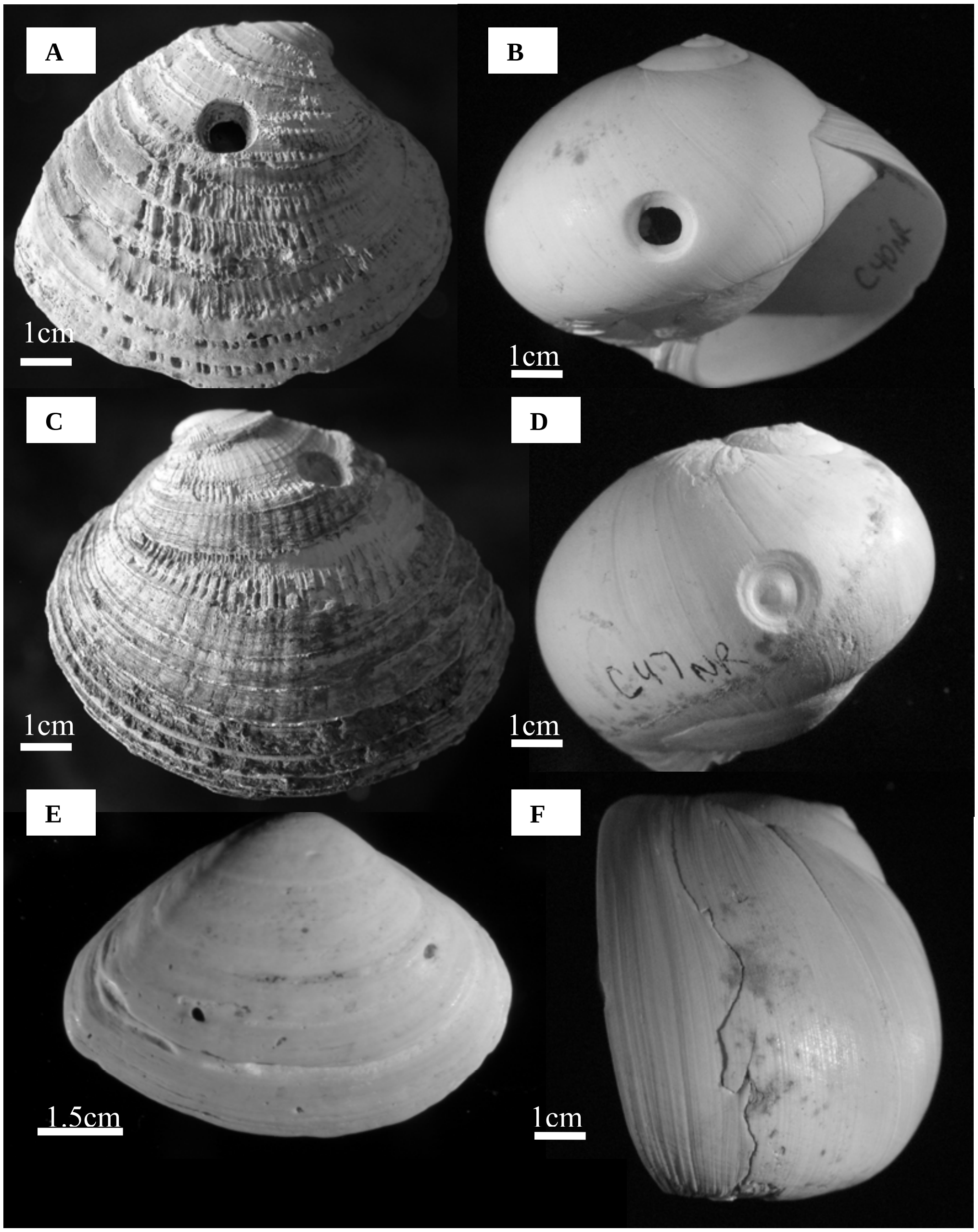

Figure 5.1: A. *Neverita duplicata* (loc. Miami Canal, FL) with a complete drill hole. B. *Chione elevata* (loc. Miami Canal, FL) with a complete drill hole. C. *Chione elevata* (loc. Punta Gorda, FL) with an incomplete drill hole. D. *Neverita duplicata* (loc. Miami Canal, FL) with an incomplete drill hole. E. *Spisula solidissima* (loc. Neuse River, NC) with repair scar parallel to the growth lines. F. *Neverita duplicata* (loc. Miami Canal, FL) with repair scar near the aperture.

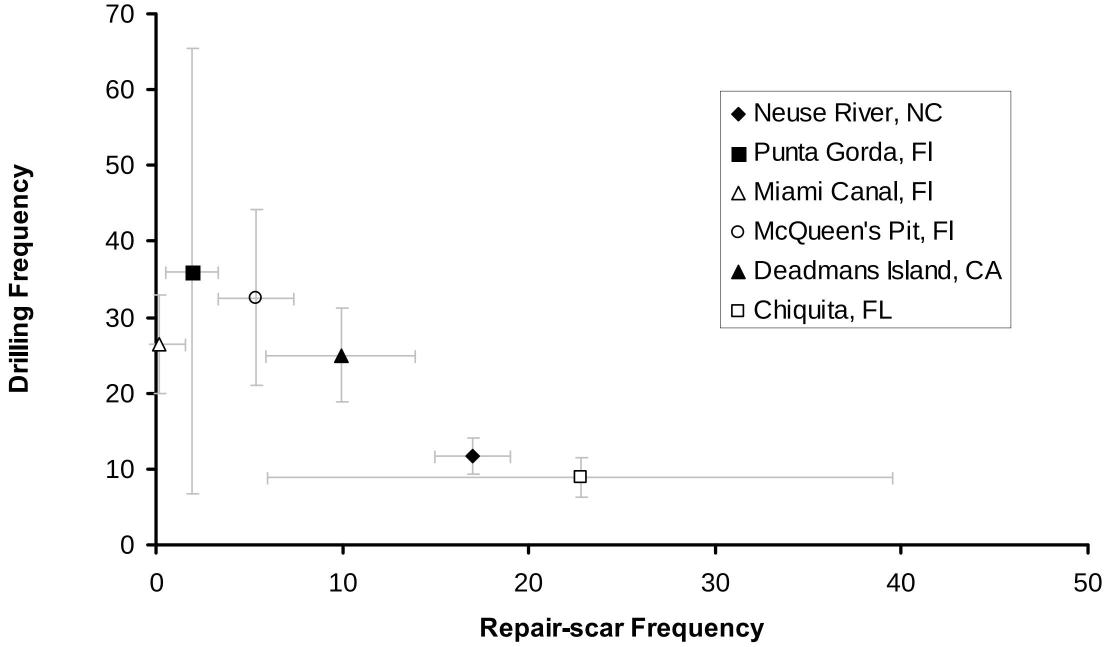

Figure 5.2: Plot showing the relationship between average repair-scar frequencies and drilling frequencies for bivalves specimens for six localities. The error bars indicate standard error for frequencies of repair-scar and drilling.

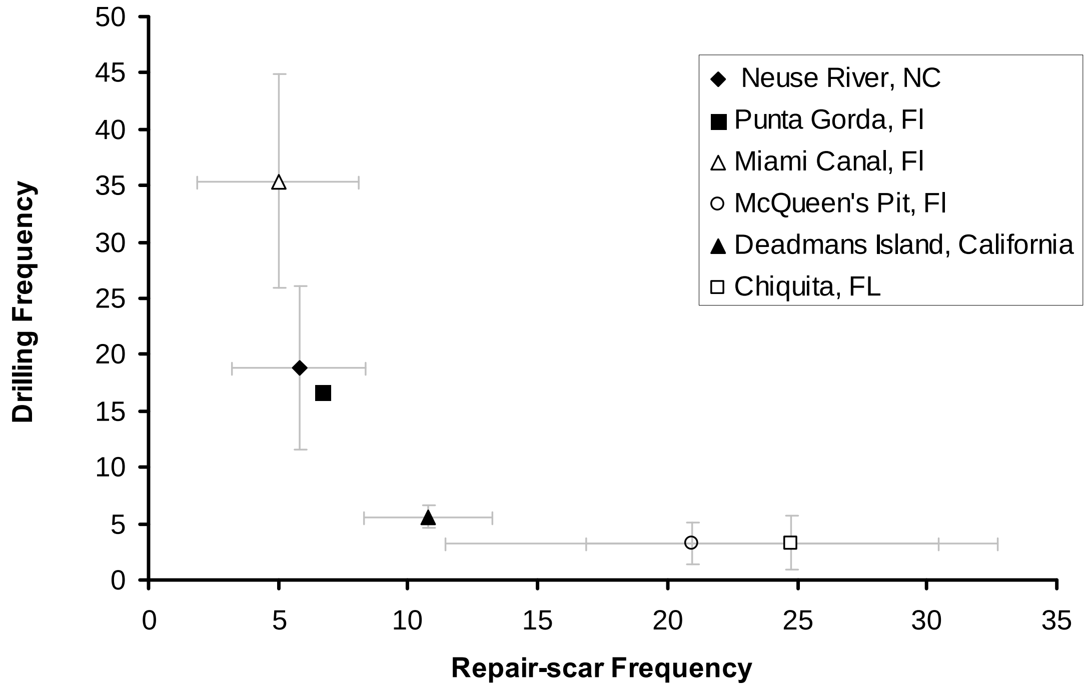

Figure 5.3: Plot showing the relationship between average repair-scar frequencies and drilling frequencies for gastropods specimens for six localities. The error bars indicate standard error for frequencies of repair-scar and drilling. Note there is no error bars associated to the point representing Punta Gorda, FL since we had only one gastropod taxon from there.

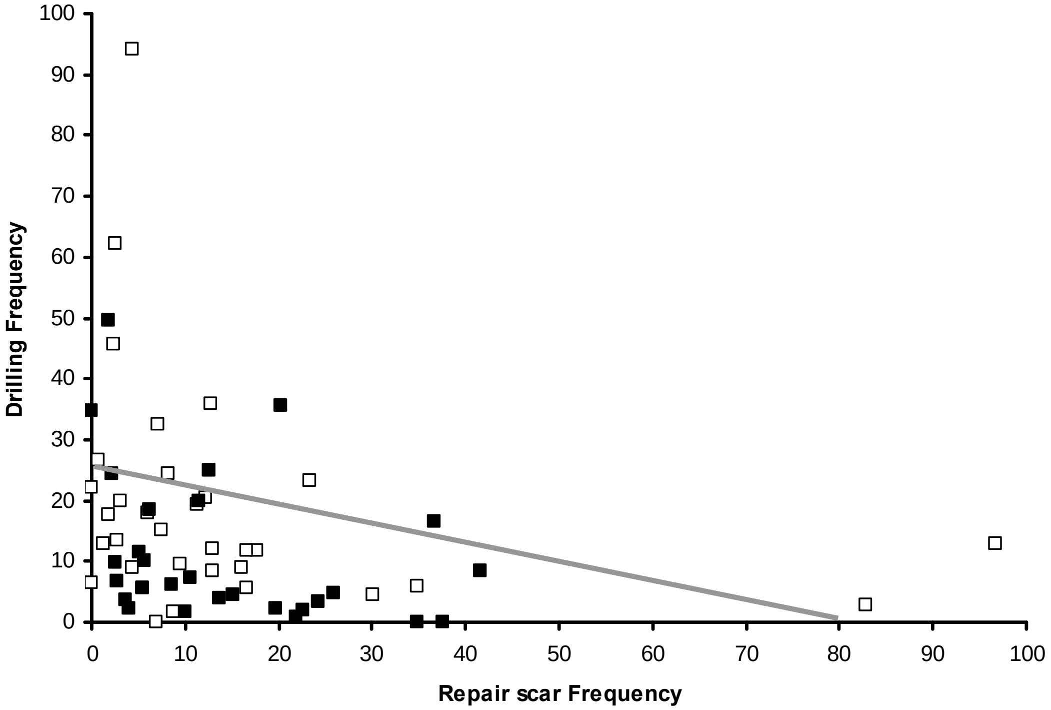

Figure 5.4: Plot showing the relationship between repair-scar frequencies and drilling frequencies for all the groups. Bivalves are represented by open squares and gastropods by solid squares.

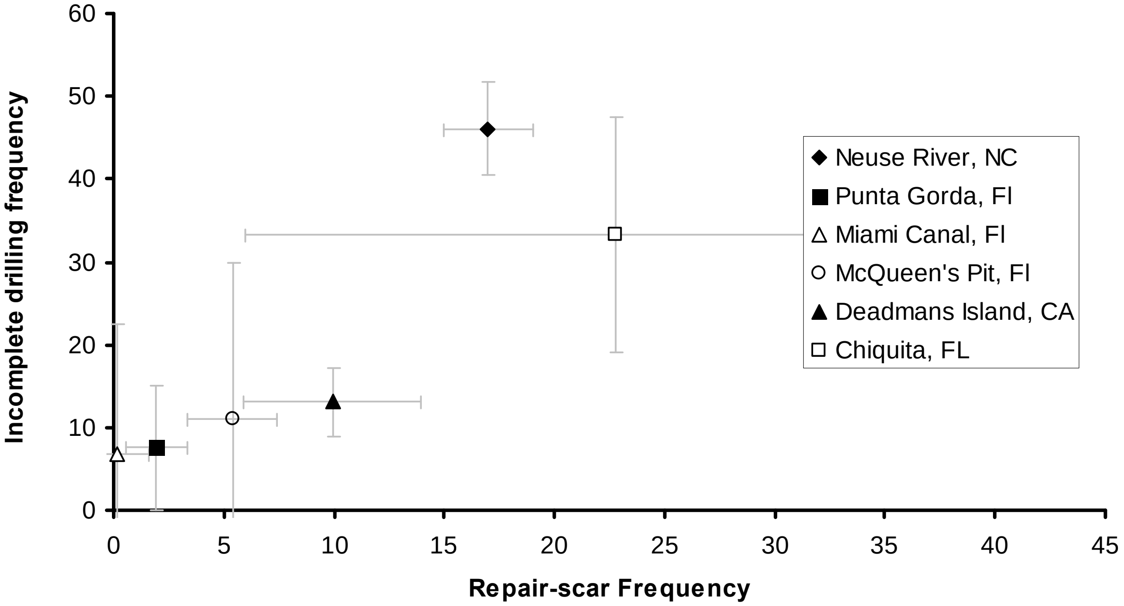

Figure 5.5: Plot showing the relationship between average repair-scar frequency and incomplete drilling frequency for bivalves specimens for six localities. The error bars indicate standard error for frequencies of repair-scar and incomplete drilling.

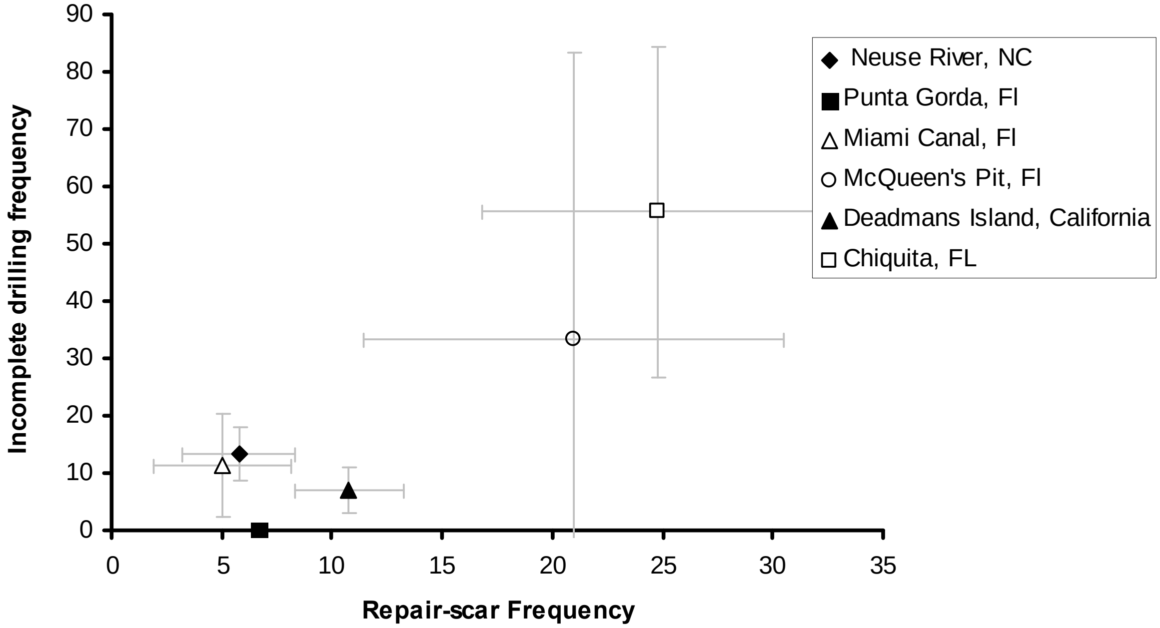

Figure 5.6: Plot showing the relationship between average repair-scar frequency and incomplete drilling frequency for gastropods specimens for six localities. The error bars indicate standard error for frequencies of repair-scar and incomplete drilling. Note there is no error bars associated to the point representing Punta Gorda, FL since we had only one gastropod taxon from there.

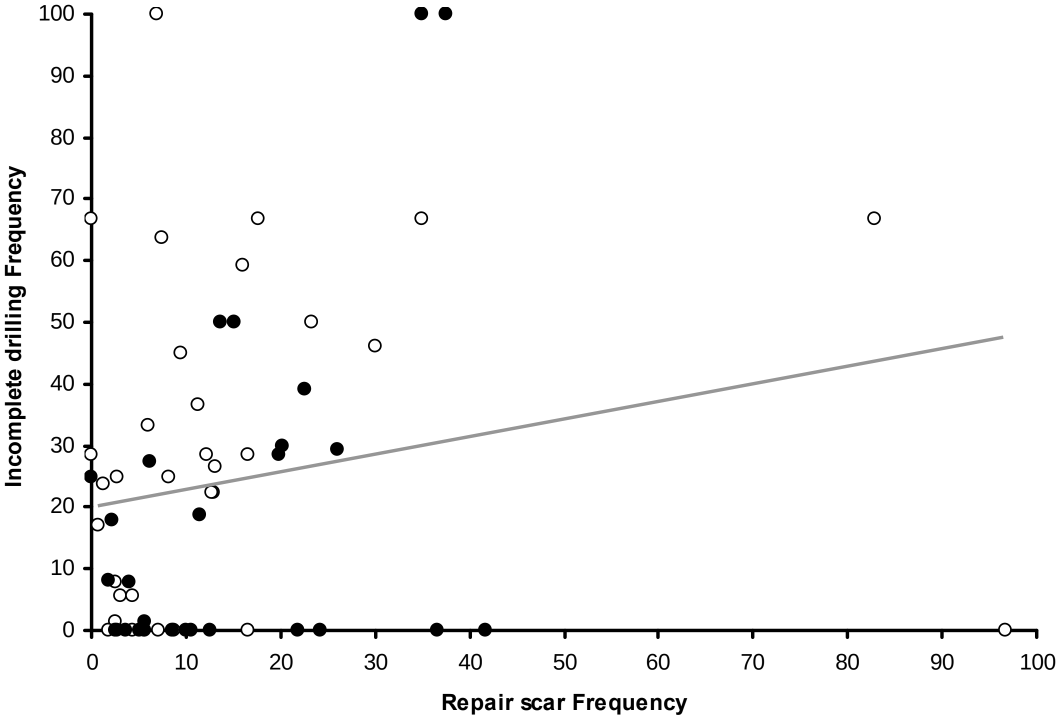

Figure 5.7: Plot showing the relationship between repair-scar frequency and incomplete drilling for all the groups. Bivalves are represented by open circles and gastropods by solid circles.

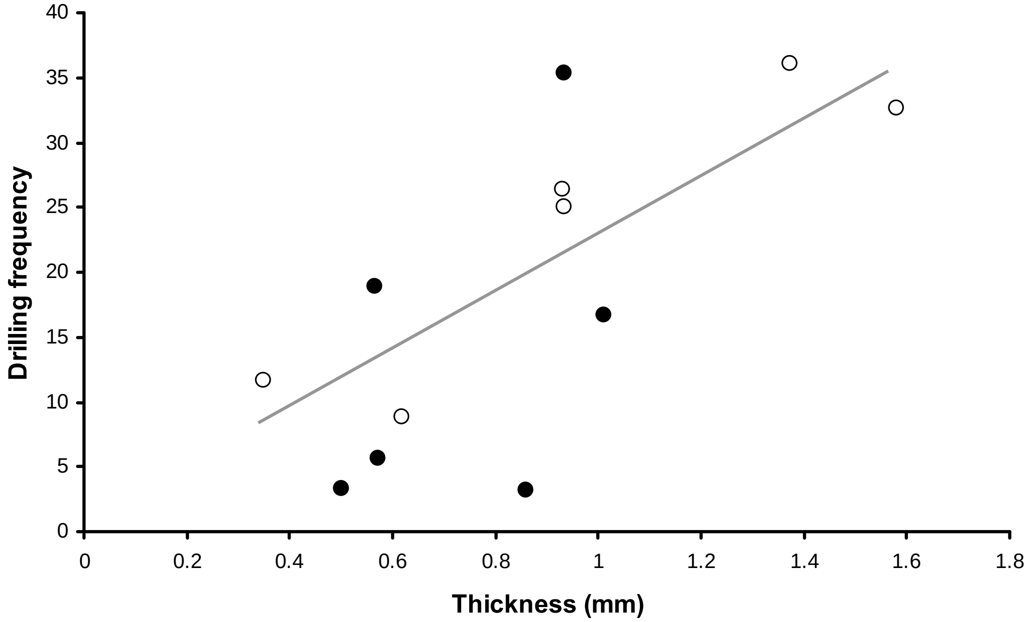

Figure 5.8: Plot showing the relationship between average shell thicknesses and drilling frequency. Open circles represent bivalves and solid circles represent gastropods.

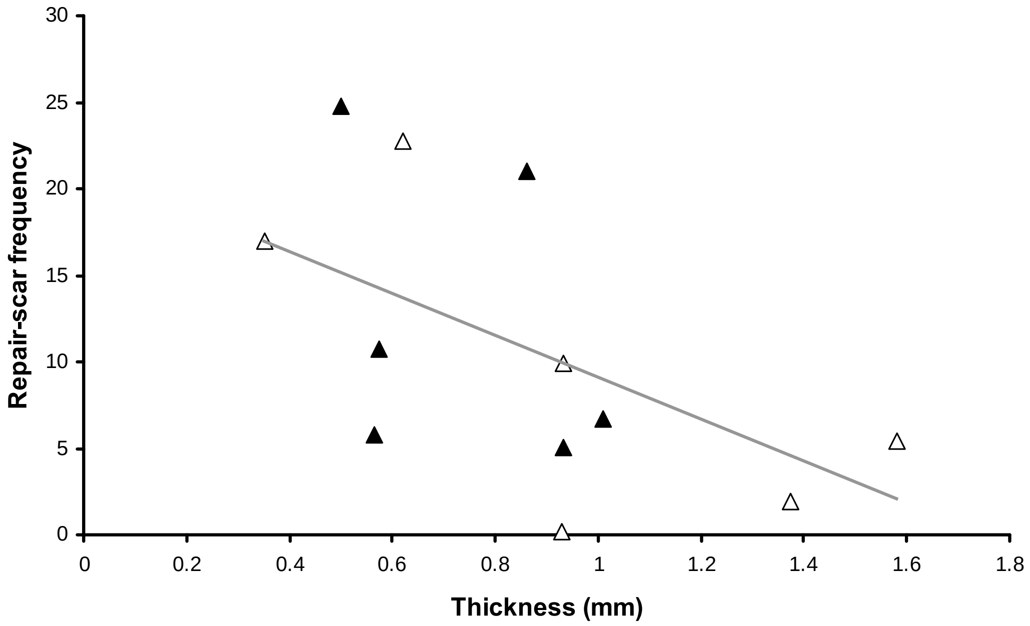

Figure 5.9: Plot showing the relationship between average shell thickness and repair scar frequency. Open triangles represent bivalves and solid triangles represent gastropods.

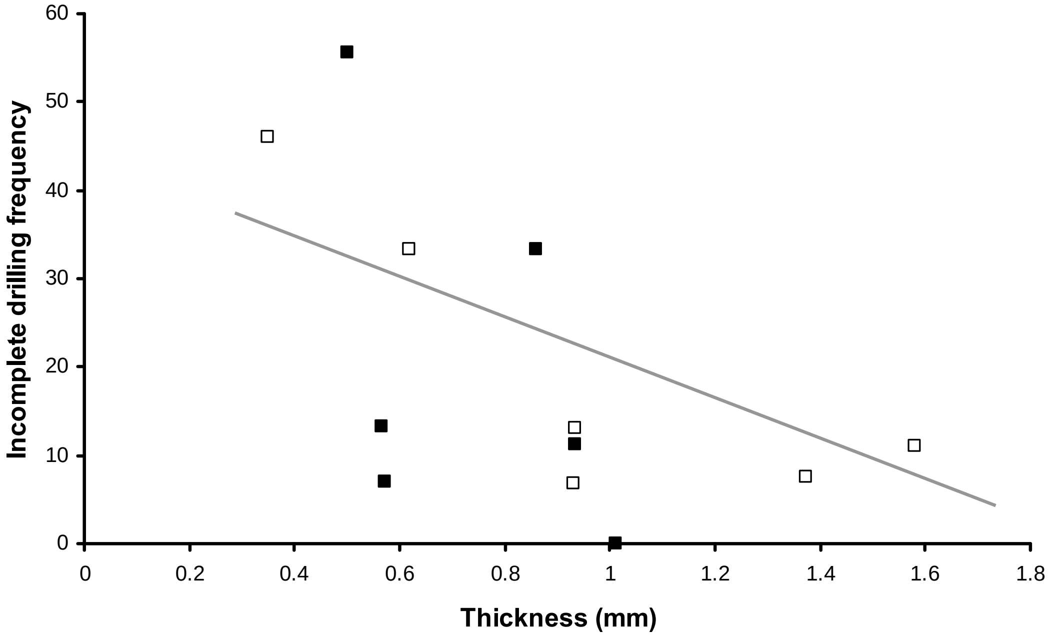

Figure 5.10: Plot showing the relationship between average shell thickness and incomplete drilling. Open squares represent bivalves and solid squares represent gastropods.

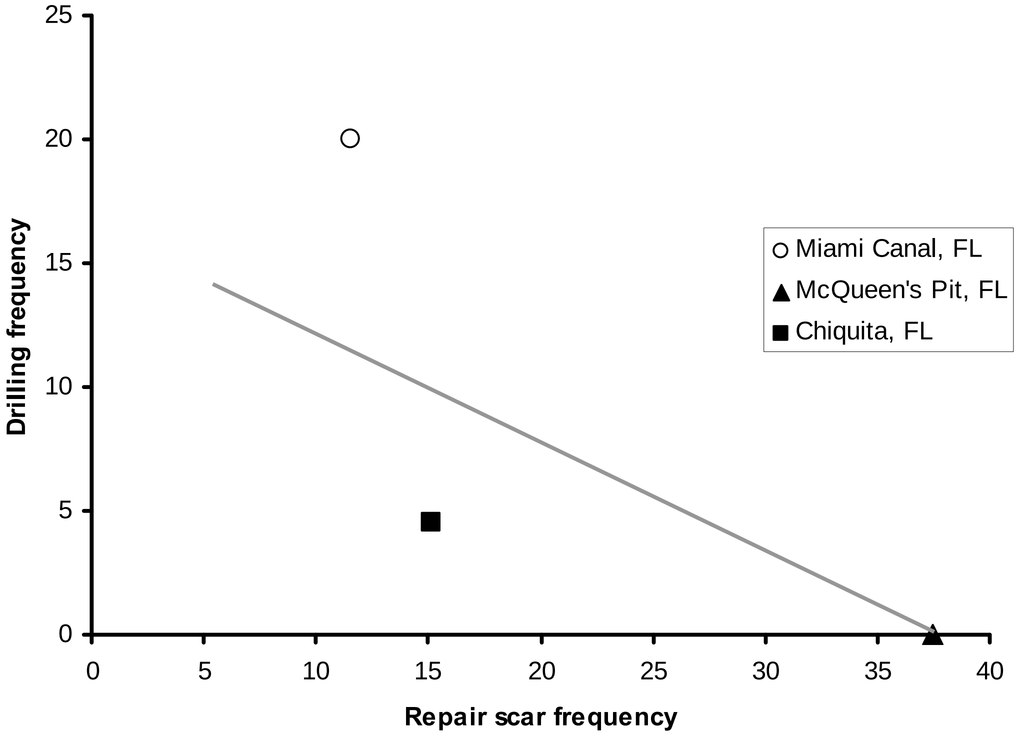

Figure 5.11: Plot showing the relationship between repair-scar and drilling frequency for *Neverita duplicata.*

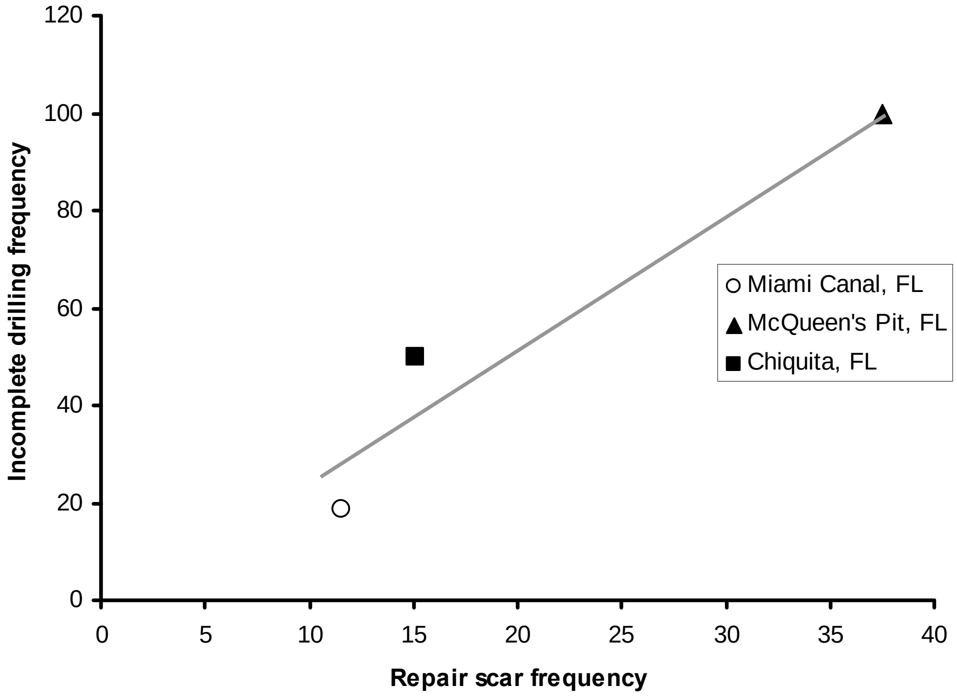

Figure 5.12: Plot showing the relationship between repair-scar frequency and incomplete drilling for *Neverita duplicata.*

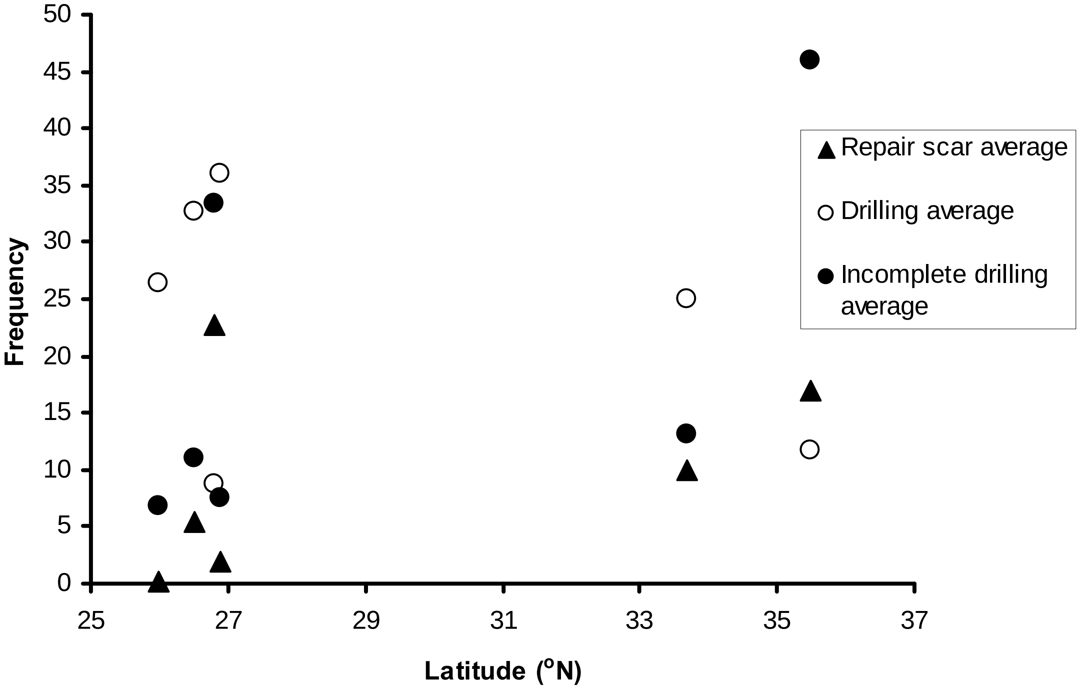

Figure 5.13: Plot showing the relationship between latitude of the localities and the average frequencies of drilling, repair-scar and incomplete drilling of bivalves.

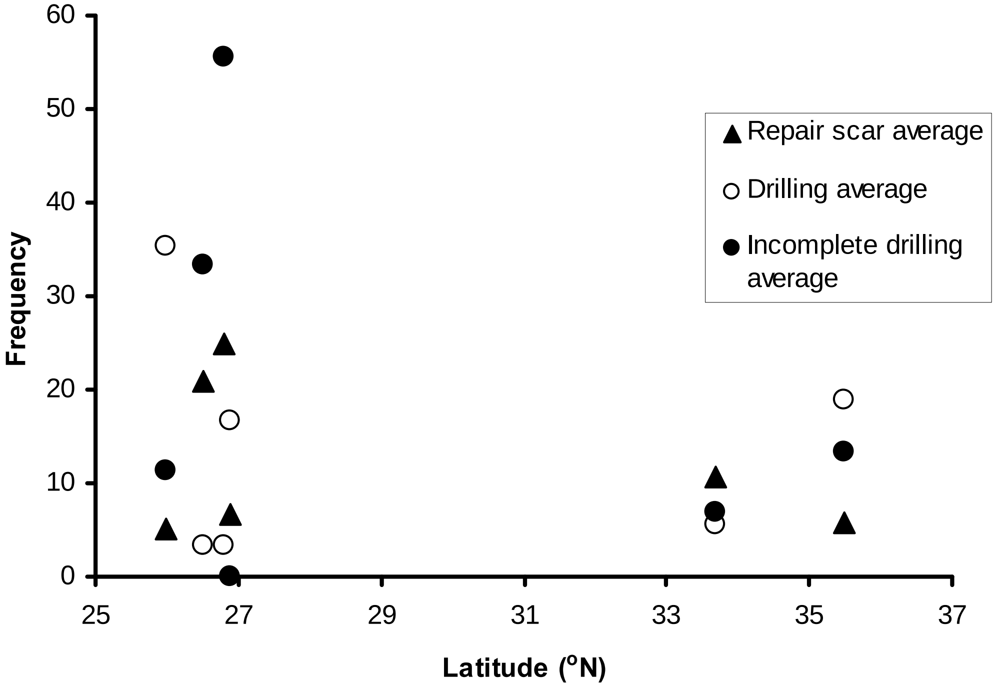

Figure 5.14: Plot showing the relationship between latitude of the localities and the average frequencies of drilling, repair-scar and incomplete drilling of gastropods.

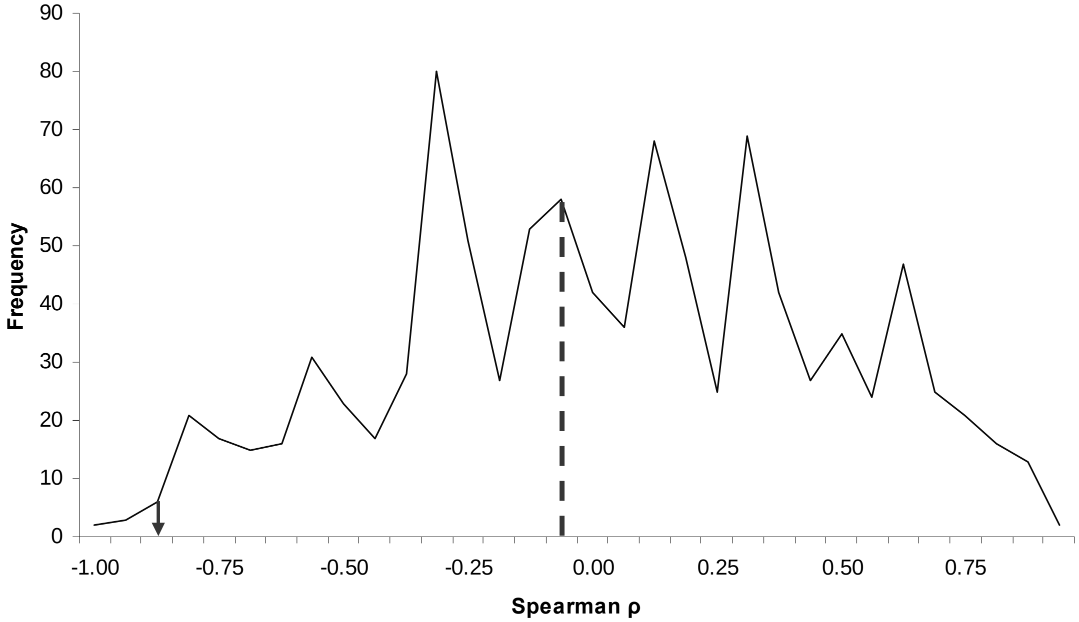

Figure 5.15: Results of simulation run for estimating the significance of the relationship between average repair-scar frequency and drilling frequency for bivalves. The dashed line represents median of the simulation where as the solid arrow represents the observed value of spearman ρ in our study.

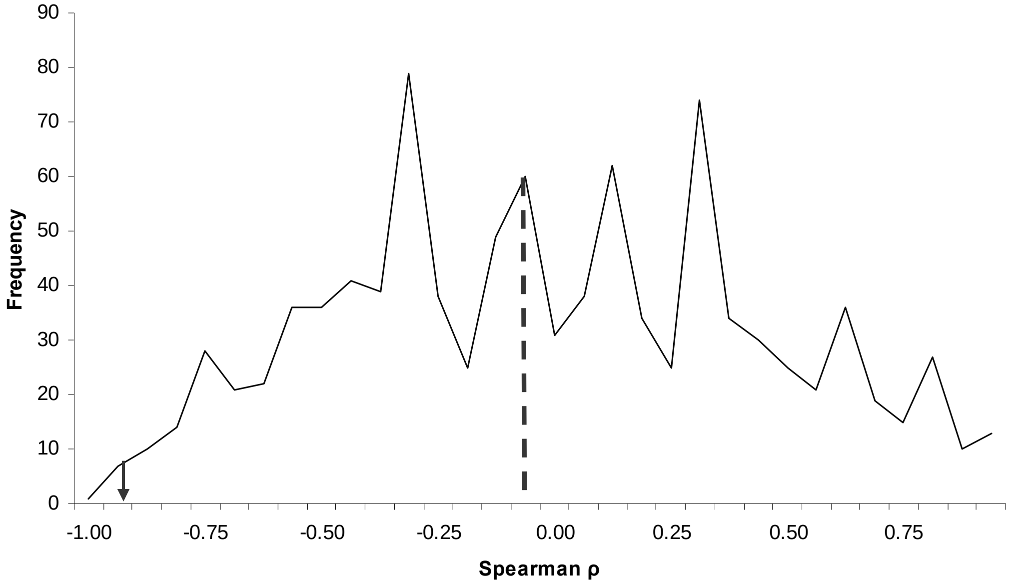

Figure 5.16: Results of simulation run for estimating the significance of the relationship between average repair-scar frequency and drilling frequency for gastropods. The dashed line represents median of the simulation where as the solid arrow represents the observed value of spearman ρ in our study.

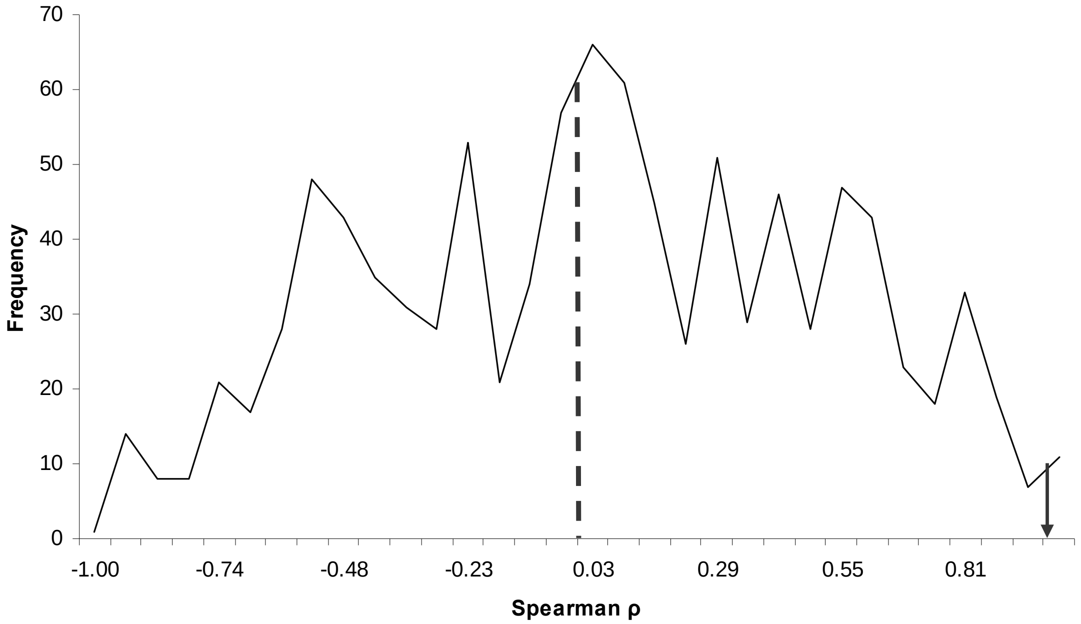

Figure 5.17: Results of simulation run for estimating the significance of the relationship between average repair-scar frequency and incomplete drilling for bivalves. The dashed line represents median of the simulation where as the solid arrow represents the observed value of spearman ρ in our study.

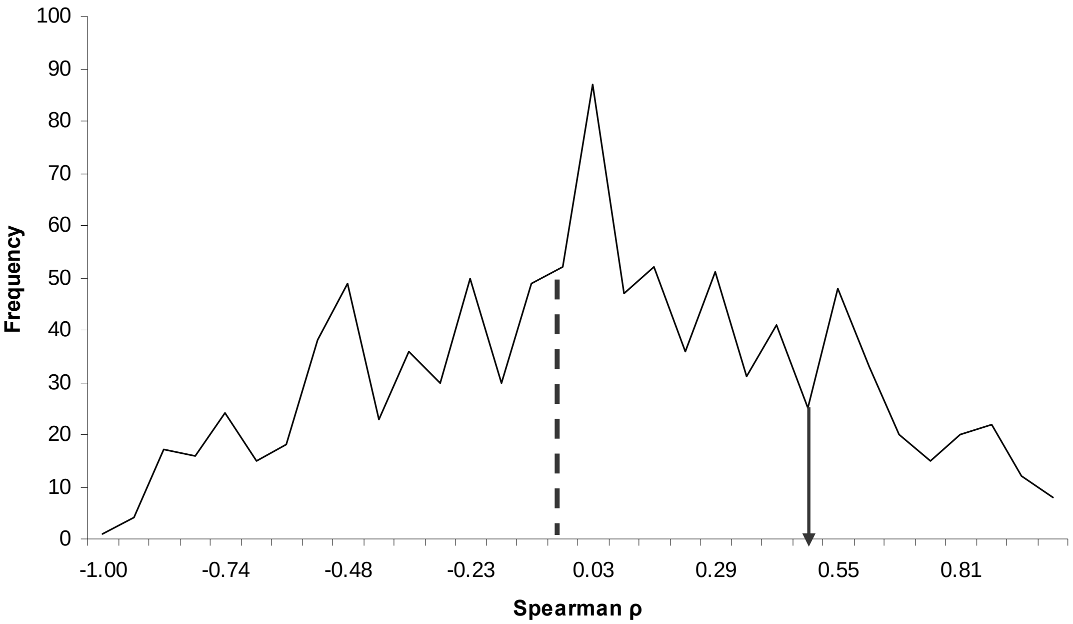

Figure 5.18: Results of simulation run for estimating the significance of the relationship between average repair-scar frequency and incomplete drilling frequency for gastropods. The dashed line represents median of the simulation where as the solid arrow represents the observed value of spearman ρ in our study.

CHAPTER 6

CENOZOIC HISTORY OF DRILLING PREDATION: A MULTI-TAXON APPROACH

Introduction

Biotic interactions have been considered a key factor in the process of natural selection and thought to play an important role in the evolution of ecosystems. The role of biotic interactions, especially predation, in shaping community structure is evident in modern marine ecosystem. However, the long term evolutionary implications of these interactions are quite controversial. Predation has been claimed to be an important driving force of evolutionary change by some; for example, Vermeij (1977) proposed that a middle Mesozoic increase in predation resulted in a restructuring of shallow marine ecosystems, a hypothesis that has received much support (Aronson & Blake, 2001; Bottjer & Jablonski, 1988). Signor and Brett found a similar trend in the mid-Paleozoic (Signor & Brett, 1984). Gould (1985) on the other hand, argued that interactions between organisms act in the ecological moments (the first tier), but can be undone, diluted, or reversed by processes operating at the second (such as speciations /extinctions) and third tier (mass extinctions) (Gould, 1985). As a result, Gould claimed that interactions of the first tier do not influence evolutionary trends of a lineage. More recently, Madin *et al.* (2006a) evaluated the effect of biotic interactions for the Phanerozoic by testing what they considered as the key predictions of the hypothesis of escalation. They interpreted the patterns of diversity of predators and prey as inconsistent with the hypothesis of escalation, but the validity of their approach has been debated subsequently (Roopnarine *et al.*, 2006; Dietl & Vermeij, 2006; Madin *et al.*, 2006b). It does not appear that resolution of the debate about the evolutionary impact of biotic interactions will be reached anytime soon. Easier to track are questions about the intensity of predation over geologic time and the causes of these changes. Perhaps most amenable to this are studies focusing on drilling predation, because it is less ambiguous than records of other forms of predation. In this study, I explored the record of Cenozoic drilling predation in the context of the diversity of drilling predators and of secondary, durophagous predators.

History of predatory drilling:

Predatory drill holes may date back to the late Precambrian (Zhao, 1992) and have been reported from various Paleozoic assemblages (Conway Morris and Bengston, 1994; Rohr, 1991; Kowalewski *et al.*, 2000). In most cases, the identities of the Paleozoic drilling predators are unknown (but see Baumiller, 1990, 2001) since the primary drillers of modern mollusks, naticids and muricids, did not begin to diversify until the Cretaceous (Sohl, 1969; Kabat, 1990). Although predatory drilling behavior is known within families of gastropods, octopods, flatworms and nematodes, most drillholes reported in molluscs resemble those made by the naticid or muricids gastropods. The earliest report of a hole similar to a naticid drillhole comes from Triassic (Newton, 1983; Fursich & Jablonski, 1984). Harper *et al.* (1998) reported muricid like drillhole from Jurassic. Body fossil of these predatory families are unknown before Cretaceous.

Behavior of drilling predators:

A number of studies have analyzed the change in drilling behavior through time, in terms of bore hole position (Berg, 1978; Kitchell, 1986, Dietl *et al.*, 2001), size selectivity (Dietl & Alexander, 2000), and taxon selectivity (Kitchell *et al.*, 1981). Generally, predatory behavior of drilling gastropods has been explained from the perspective of a two-taxon system. However, the behavior of drilling gastropods can be influenced by their own predators and by other predators on their prey. The interaction between different predatory groups and the resulting “emergent effect” has been a topic of discussion in the ecologic literature for last couple of decades (Sih *et al.*, 1985, 1998; Lima *et al.*, 1990). Given that natural communities typically have multiple predators feeding on most prey, understanding emergent multiple predator effects (MPEs) is a critical issue for community ecology (Wilbur *et al.*, 1990; Wooton, 1994). These studies suggest two main types of emergent effects–1) risk reduction caused by predator–

predator interactions and 2) risk enhancement caused by conflicting prey responses to multiple predators. In a recent laboratory experiment to assess the effect of a secondary predator on the behavior of a drilling gastropod, we found a significant change in drilling behavior: in the presence of a secondary predator the success rate decreased resulting in a decrease in overall drilling frequency and an increase in incomplete drilling frequency (increase in prey-effectiveness) (Chattopadhyay & Baumiller, 2007). Trying to evaluate this hypothesis in the fossil record is complicated because a reliable proxy for the activity of secondary durophagous predator is required. We used repair marks as proxy for durophagous predation, and found patterns consistent with the neontologically-derived hypothesis for Plio-Pleistocene assemblage (Chattopadhyay & Baumiller, 2008).

If the effect of secondary durophagous predators on drilling predators is general, then one ought to expect an inverse coupling between drilling frequency and durophagous activity even over broader time spans. If secondary predators do not significantly impact drilling predators, drilling frequencies might be primarily affected by some other factor, such as the diversity of drillers. In this study, using Cenozoic data on predation intensity (Huntley and Kowalewski, 2007) and diversity data from the Palobiology Database (PaleoDB), I explore the relationship between drilling predation intensity and 1) the diversity of drilling predator and 2) the activity of durophagous predator, as measured by repair scar frequencies.

Materials and methods

Data:

The predation database for marine invertebrates compiled by Huntley and Kowalewski (2007) was used in this study. It provides methodologically consistent species-level estimates of trace fossil frequencies. It also includes a sufficient number of estimates based on bulk samples to assemble a time series of predation intensity estimates. The original database was created using literature and previous data surveys (196 publications total). It consists of a compilation of 2,292 occurrences of predation traces ranging in age from Ediacaran to Holocene. Only data for Late Cretaceous and Cenozoic period were used in this study. Analyses were restricted to species-level frequency data on predatory drill holes and repair scars reported from bulk samples with *n* >=10 specimens per prey species. The restricted dataset includes a total of 748 species-level estimates of predation intensity, including 112 estimates of repair scars, interpreted as durophagous predatory events, and 636 estimates of drilling, assumed to represent successful drilling predation events.

The PaleoDB was used to construct genus level diversity of different predatory groups. Predatory gastropod diversity was obtained from Cretaceous to Pleistocene by using the 6369 occurrences of naticid, muricid and cassid genera (two-timers) that were resolved within seven Cenozoic epoch level bins in the PaleoDB as of 5th January, 2009. Decapod diversity was evaluated based on 586 occurrences in the PaleoDB. Genera that could not be assigned to a taxonomic order (often because they represent misspellings of valid genera), were excluded from the analysis.

Statistical analysis:

A computer simulation using resampling was developed to test the null hypothesis of no correlation between repair scar and drilling frequencies (Ho: Slope $_{\text{repair scar-drilling}}$ = 0). The simulation is used to compare the observed trend to one produced by chance. In each simulation, drilling frequency data for each time bin are generated by randomly choosing drilling frequencies from the list of observed drilling frequencies from all the time bins. For instance, there are four reported data points for drilling frequencies in the Eocene. In each simulation, for the Eocene, four drilling frequency data were randomly chosen from that entire list of drilling frequencies, and a simulated Eocene median drilling frequency was calculated. The same procedure was used to generate a median repair scar frequency for the Eocene. Once simulated frequencies had been generated for all the time bins, a least squares linear regression was fit to the drilling and repair scar frequencies and the slope of the regression was calculated. By running the simulation1000 times, a frequency distribution of the slopes was obtained, and this was compared to the slope of the regression for the observed data. The same approach was used to explore the relationship between repair scar frequency and 1) overall drilling frequency, 2) naticid drilling frequency. There were not enough data to apply this approach for muricid drilling frequencies.

Results

The diversities for different epochs were normalized for epoch duration by dividing the number of sampled genera by the duration of the epoch. Normalized diversities of predators through time are not correlated with drilling predation intensities (Fig. 6.1). This is also true when naticid generic diversity is compared to naticid drilling frequencies (Fig.6.2). However, normalized decapod diversity is significantly correlated with over all repair scar frequencies ($p = 0.05$) (Fig. 6.3). Also, a negative relationship characterizes repair scar and drilling frequencies: it is not significant for all gastropod data (Fig.6.4, 6.5, 6.6), but it is significant for naticid gastropod drillholes ($p = 0.05$) (Fig.6.7, 6.8, 6.9).

Discussion

A number of studies have uncovered an increase in drilling predation during the Cretaceous, reaching modern-day levels by the Late Cretaceous/Cenozoic (Dudley and Vermeij, 1978; Taylor *et al.*, 1983; De Cauwer, 1985; Allmon *et al.*, 1990; Kelley and Hansen, 1993, 1996a, b; Harper, 1994; Hagadorn and Boyajian, 1997). Predation intensity appears to have stabilized during the Neogene (Thomas, 1976; Tull and Bohning-Gaese, 1993). Conventionally, the post-Cretaceous rise in predation intensity has been attributed to the appearance and subsequent diversity increase of predatory gastropods, primarily naticids and muricids. The patterns obtained in this study do not support this claim. Even a more restricted look at naticids only, failed to support the claim for a correlation between drilling frequencies and predator diversity. Interestingly, the diversity of decapods does correlate with frequencies of repair scars. These patterns indicate that the activity of durophagous predators may play an important role in affecting drilling frequencies, as has been argued in previous chapters, a role that is perhaps greater than drilling predator diversity itself. Durophagous predators are, of course, likely to be impacted by their own predators (not explored in this study), but the level of interference might not overwhelm the relationship between decapod diversity and decapod predatory activity, as reflected in the record of repair scar frequencies.

This study has bearing on the theory of escalation. The theory of escalation argues that biological agents have been the chief selection pressure experienced by organisms, and over the Phanerozoic these hazards became increasingly severe (Van Valen, 1973; Vermeij, 1977). The asymmetry of the effects on predators and prey ("the dinner-death" principle), suggests that over long periods of evolutionary time it is predators that play the dominant role (Vermeij, 1987; Trussell and Smith, 2000; Dietl and Kelley, 2002). Since it is predators that lead the arms race, in a three-taxon system, there should be a top-down cascade of effects, with the lowest tier affected not only by its predators, but its predators' predators. The results of this study are consistent with this prediction.

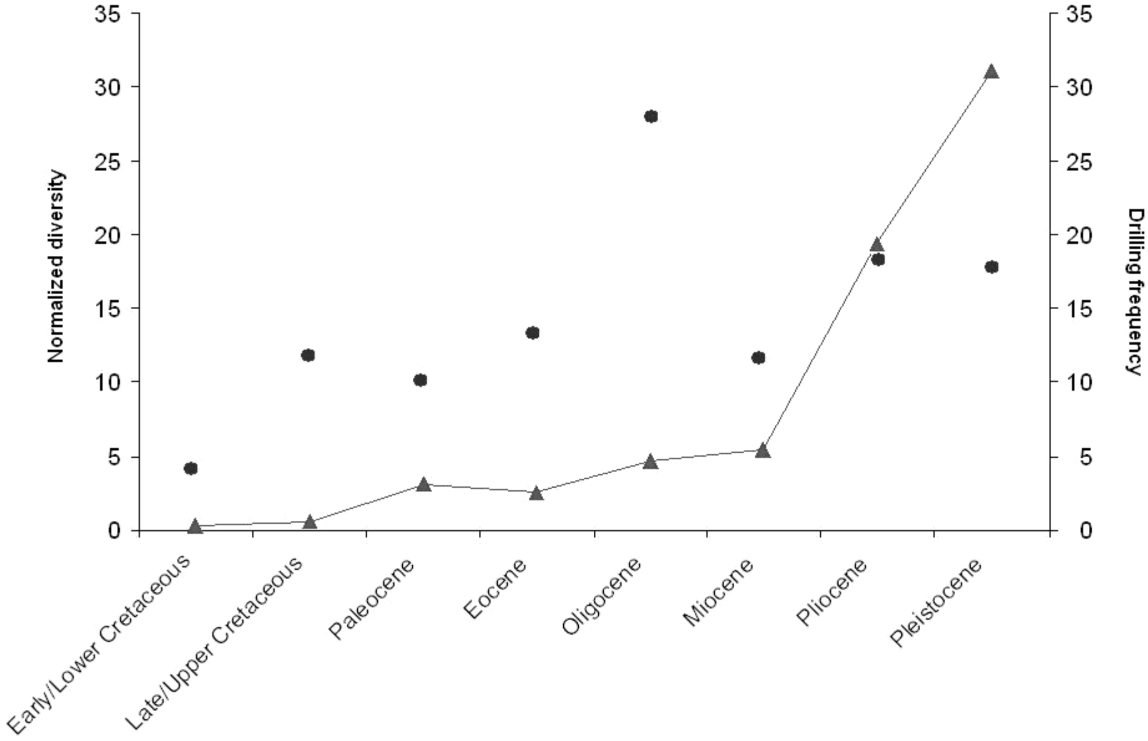

Figure 6.1: Cenozoic normalized gastropod predator diversities and median drilling frequencies. The solid line represents normalized gastropod predator diversities and the solid circles represent median drilling frequencies.

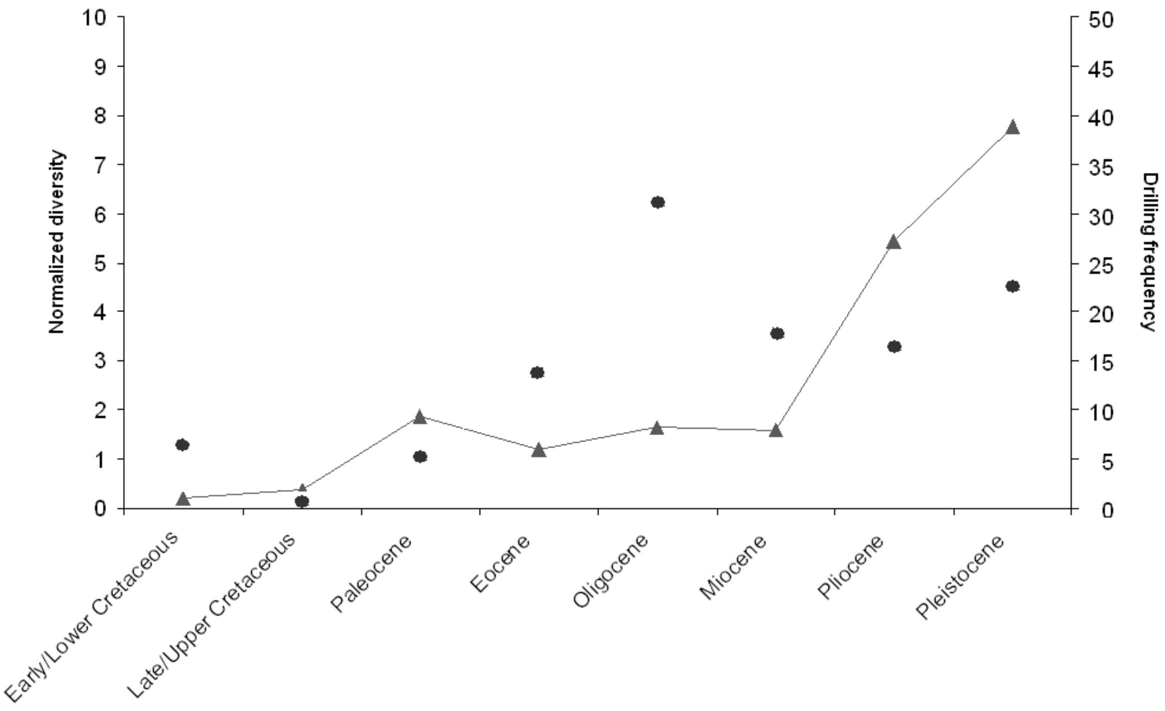

Figure 6.2: Cenozoic normalized naticid diversity and median naticid drilling frequency. Solid line represents normalized naticid diversity and the solid circles represent median naticid drilling frequency.

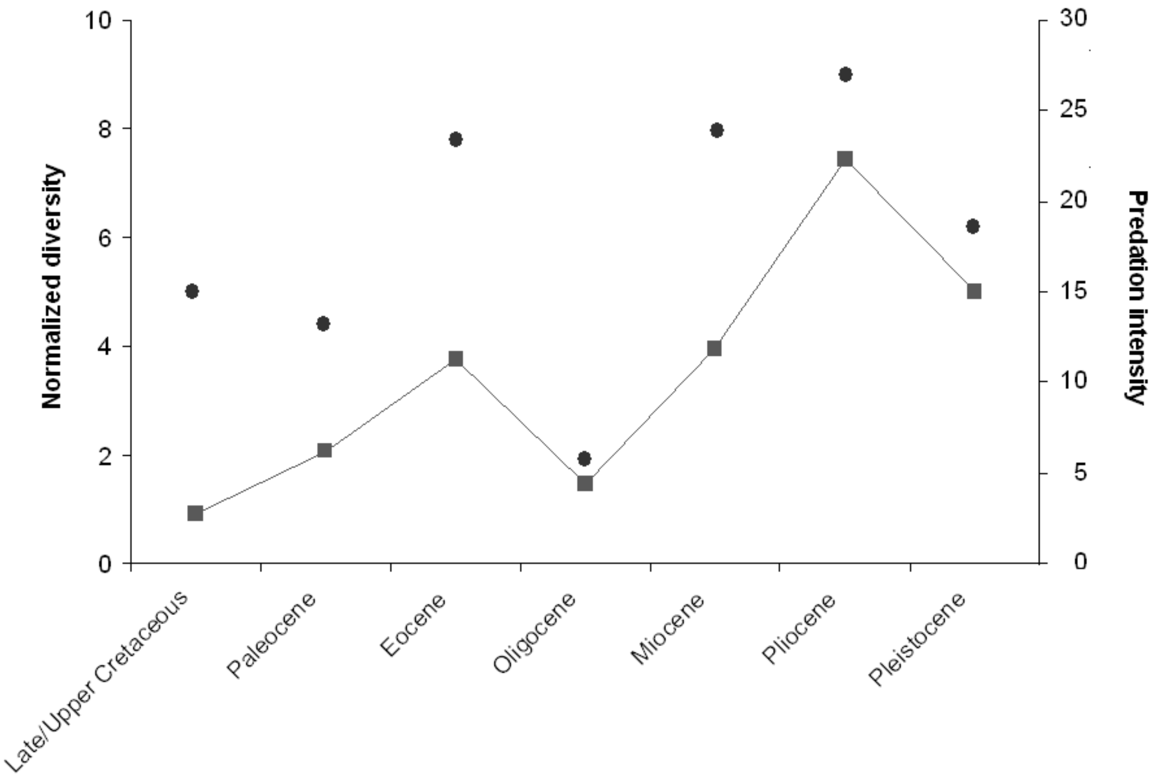

Figure 6.3: Cenozoic normalized decapod diversity and median repair scar frequency. Solid line represents normalized decapod diversity and the solid circles represent median repair scar frequency.

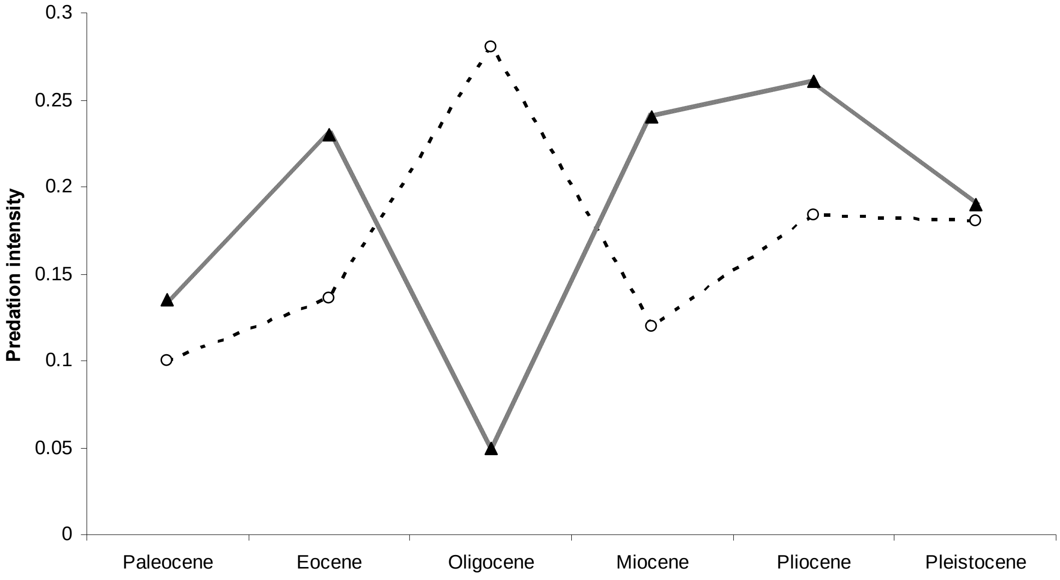

Figure 6.4: Plot showing the change in predation intensity in the Cenozoic. The solid line represents repair scar frequency and the dotted line represents gastropod drilling frequency.

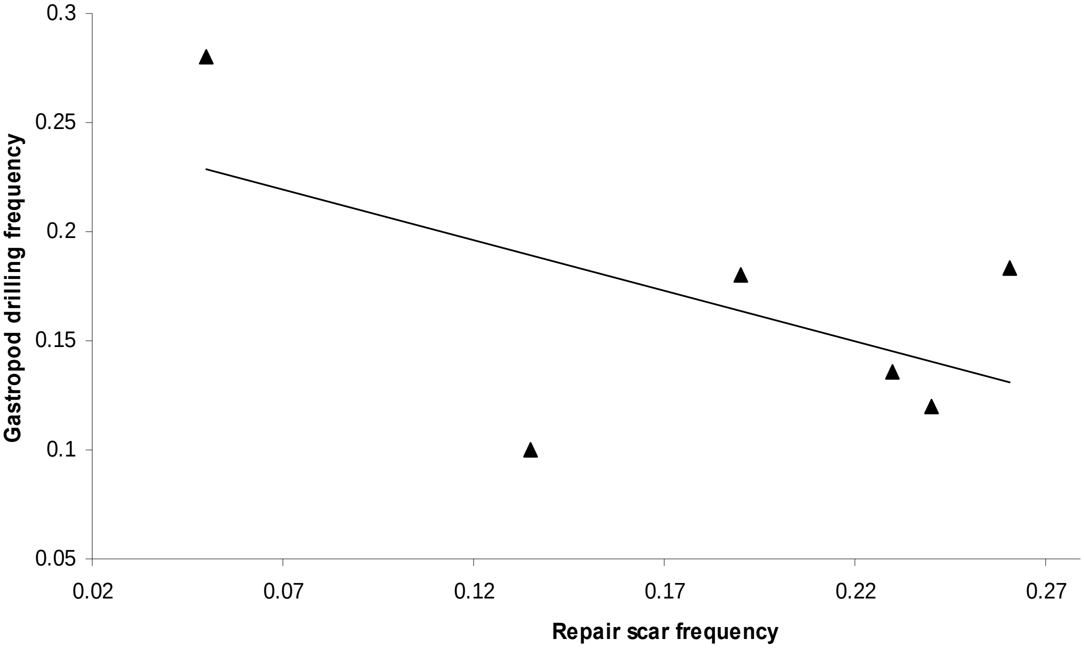

Figure 6.5: Plot showing the relationship between repair scar frequency and gastropod drilling frequency.

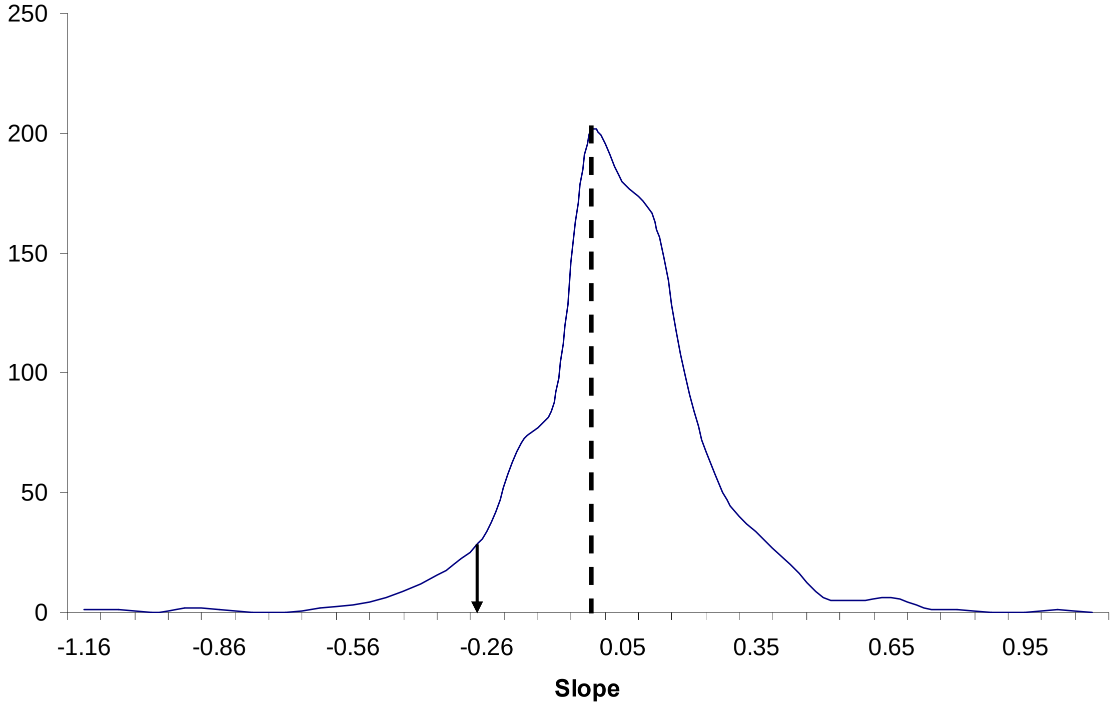

Figure 6.6: Results of simulation run for estimating the significance of the relationship between median repair scar frequency and gastropod drilling frequency. The dashed line represents median of the simulation whereas the solid line represents the observed slope.

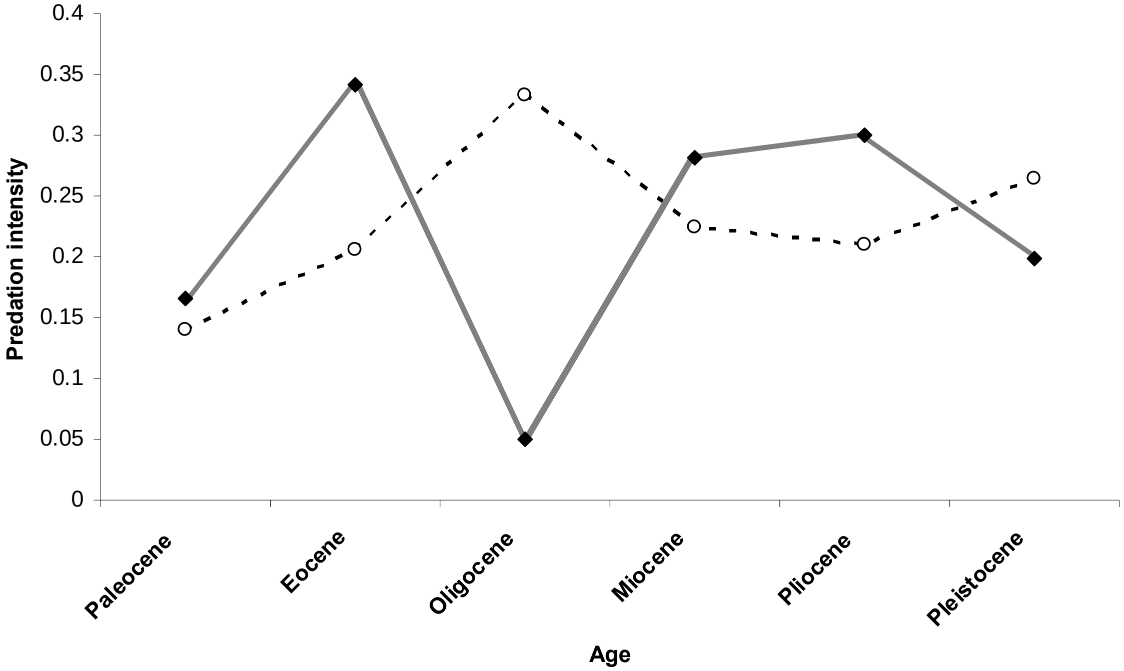

Figure 6.7: Plot showing median predation intensity in Cenozoic. The solid line represents repair scar frequency and the dotted line represents naticid drilling frequency.

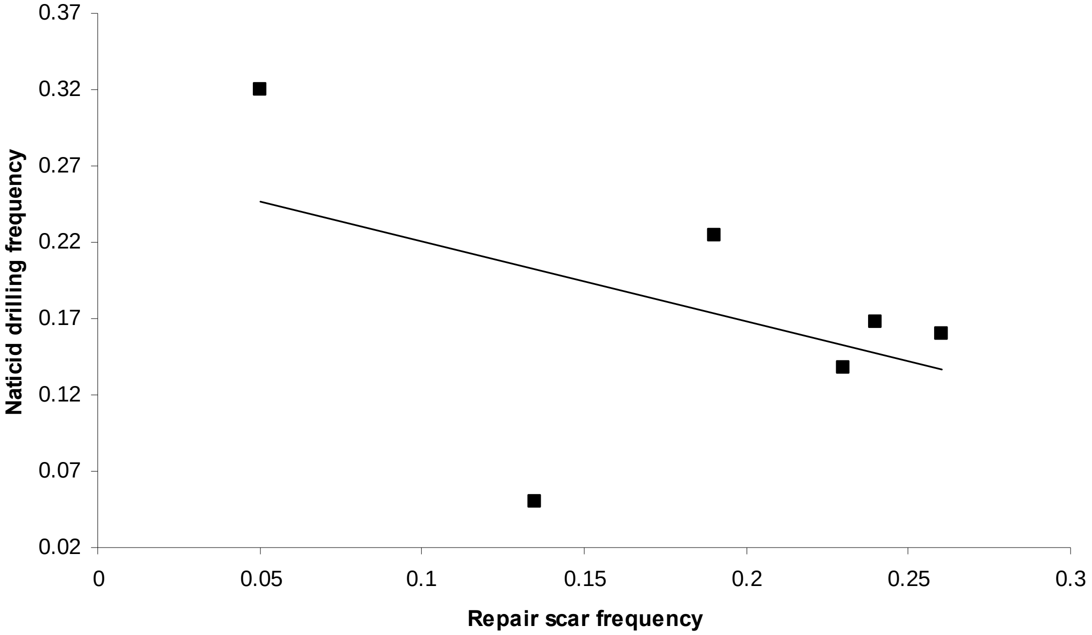

Figure 6.8: Plot showing the relationship between repair scar frequency and naticid drilling frequency.

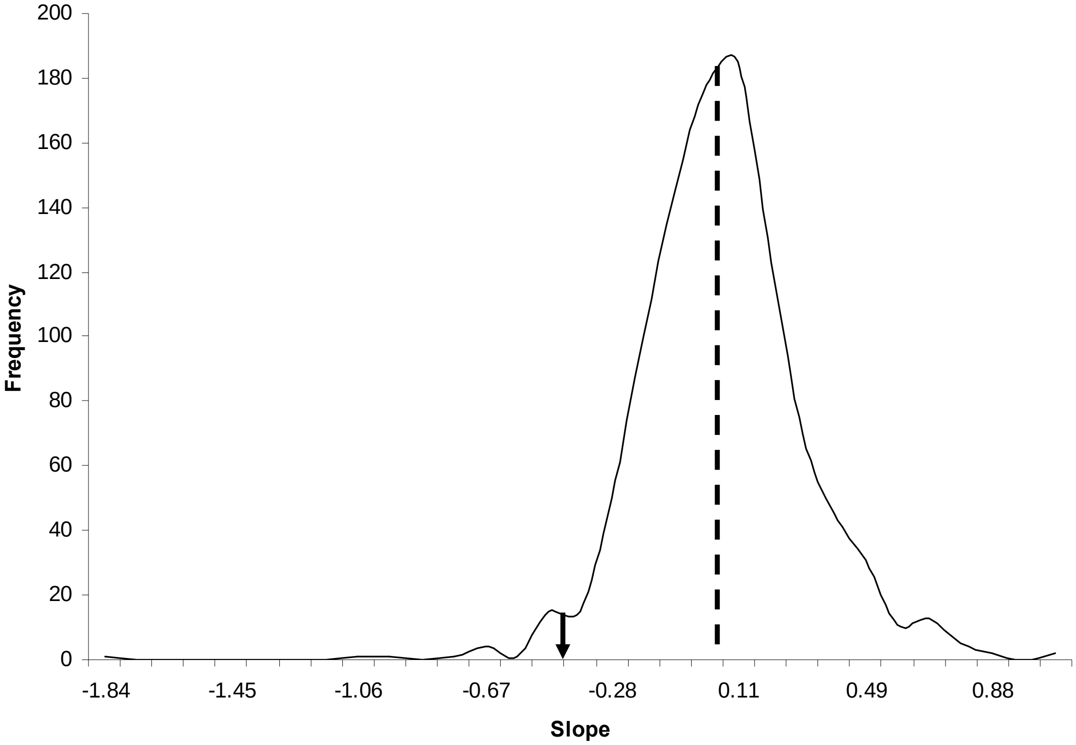

Figure 6.9: Results of simulation run for estimating the significance of the relationship between median repair scar frequency and naticid drilling frequency. The dashed line represents median of the simulation where as the solid line represents the observed value of the slope in our study.

CHAPTER 7

CONCLUSION

In modern marine environments, predation is a significant agent of natural selection. However, evidence of predation in fossils is generally rare, primarily because most predators destroy the prey or leave no traces on any preservable hard parts of the victim. Drilling predation of shelled marine invertebrates by muricid and naticid gastropods represents one of the very rare instances that allow biotic interactions to be evaluated quantitatively in the Recent and in the geologic record. The drilling predator-prey system, because it is common in modern marine environments, also has the advantage of providing researchers an opportunity for studying its details through neontological experiments. As a consequence, it provides an unparallel opportunity for testing ecological and evolutionary consequences of biotic interaction.

Although it is generally assumed that that the drilling predation data has not undergone any taphonomic change that could generate a bias, the results of Chapter II reject this assumption by exploring a potential taphonomic bias in drilling predation data. In Chapter II, I found that hydrodynamic sorting during post-mortem transportation of bivalved shells could result in a taphonomic bias. Since the hydrodynamic properties of a shell in a moving fluid depends on the presence and the location. This bias could potentially generate assemblage significantly different from the original one in terms of drilling frequency and stereotypy. I investigated one such taphonomic bias that relates to the hydrodynamic properties of shells: presence of drill holes and/or drill hole position may influence how shells behave when subjected to moving fluids. I have also constructed models to identify hydrodynamically altered assemblage.

In order to understand the past biotic interaction, it is essential to gather data on the interaction of their modern counterparts. The results of these neontological studies revealed new perspectives about the drilling predator-prey system. The results of Chapter

III about the rates of feeding and consumption are really useful for future cost-benefit analysis. I also demonstrated that the new metric, “excavation rate” better illustrates the total work done by the predator. The results indicate that although penetration rate is independent of predator size, excavation rate is proportional to the size of the driller, as one might expect on biomechanical grounds. Additionally, consumption rate is also a function of prey size which might have important implications in cost-benefit analyses.

In another neontological study, I have investigated the effectiveness of certain behavioral traits of the prey against drilling predation, namely clumping. In a joint study with M. Casey (Department of Geological Sciences, Yale University), we observed a significant decrease in the drilling frequency within the group containing clumped mussels, confirming that clumping acts as a successful anti-predatory strategy against drilling predators (Appendix). In spite of potential differences in prey handling and grappling due to clumping, mean drill-hole placement and variation in drill-hole placement showed no significant differences between the two groups. These observations suggest that comparison of predation intensities across clumping and non-clumping taxa must consider the anti-predatory effect of this behavior.

Conventionally, drilling predator-prey system has been studied from a two-taxon perspective. The results of Chapter IV demonstrates that secondary predator, such as durophages, could significantly influence the behavior of drilling predator. The results indicate that the presence of a secondary predator can affect drilling activity, leading to a significant increase in the frequency of incomplete drill holes. The introduction of a secondary predator can also decrease the overall drilling frequency. The size distributions of completely and incompletely drilled mussels suggest that in the presence of the secondary predator the decision by the gastropod to either abandon or continue drilling its prey might be influenced by how much time it has already invested into drilling or the size of the prey item. These results are important for the ecological and evolutionary implications of incomplete drill holes frequencies, especially with regard for their use as proxies for evolutionary prey improvement.

I extended the results of this neontological experiment to fossils. I tested whether the effect of secondary predators on drilling frequencies can be detected in the fossil record. In Chapter V, I found that repair scar frequencies, a proxy for activity of durophagous predators, correlate directly with incomplete drill hole frequencies and inversely with complete drill hole frequencies. These results suggest that the activity and success of drilling predators is influenced not just by the prey, but also by secondary predators.

I extended my previous findings in a broader temporal scale and tested whether or not these ecological interactions could be identified in a global data set of broad temporal span. The results of Chapter VI, demonstrates that there is an inverse correlation between durophagous predation and drilling predatory activity for Cenozoic. I have also found that the fluctuation in drilling predation intensity over Cenozoic can not be explained by the change in diversity of predatory gastropod groups.

These studies demonstrate the importance of biotic interaction both in modern as well as ancient ecologic communities. Drilling predators and their enemies provide a unique opportunity to study complicated ecological networks of the past and its evolutionary consequences.

APPENDIX

CLUMPING BEHAVIOR AS A STRATEGY AGAINST DRILLING PREDATION: IMPLICATIONS FOR THE FOSSIL RECORD

Introduction

Predatory drill-holes in marine invertebrates are of great interest to paleontologists, because they represent an important source of information on the nature of biotic interactions from the past that can be studied and analyzed quantitatively (Kitchell, 1986). In addition, both prey and predator have high preservation potential and extensive fossil records. The drilling gastropod-bivalve system allows paleontologists to test evolutionary hypotheses over geologic time, while modern laboratory experiments can provide an important biological context and be used to constrain what information can be reliably obtained from the fossil record of drill-holes (e.g., predator size (Kowalewski, 2004), predator identity (Kabat, 1990), rates of predator success (Dietl, 2000), and prey-size selectivity (Dietl and Alexander, 1995)).

Clumping behavior in mussels (Fig. Ap.1) has been shown to act as a successful anti-predatory defense against crushing predators like crabs and lobsters (Okamura, 1986; Lin, 1991). This interpretation of clumping behavior is further supported by experimental evidence showing that exposure to chemical cues derived from crushing predators can induce clumping behavior (Coté and Jelnikar, 1999) and increased number and diameter of byssus threads produced by the mussel *Mytilus edulis* (Coté, 1995). Okamura (1986) showed that risk of crushing predation is lowest for individuals on the interior of clumps where the negative effects of aggregate living are highest (Bertness and Grosholz, 1985). Aggregate living is ubiquitous in natural populations of mussels in spite of the reduced growth rate and decreased fecundity experienced by aggregated mussels, especially those in the center (Bertness and Grosholz, 1985). The mussels experience a trade-off between the negative effects of living in clumps and the protection afforded by aggregate living.

The relative cost of such a trade-off would be minimized if clumping acted as an anti-predatory defense against additional types of predators such as drilling gastropods. Okamura (1985) hypothesized that clumping would not be effective against drilling predators, but this hypothesis has not been tested. The first aim of this study is to test the efficacy of clumping behavior as an anti-predatory strategy against drilling gastropod predators in a laboratory using the mussel *Mytilus trossulus* (Gould) and the drilling muricid gastropod *Nucella lamellosa* (Gmelin).

The consistency of drill-hole placement on prey shells (drill-hole stereotypy) and the drill-hole's correspondence to internal anatomy have been used to infer important information about predator behavior in the fossil record (Kelley and Hansen, 2003 and references therein). A number of previous experimental studies involving muricid gastropod and mussels show somewhat contradictory results regarding drill-hole stereotypy. Rovero *et al.* (1999) and Dietl (2000) both found a significantly non-random distribution of drill-holes, when examining the muricid *Nucella lapillus* preying on the mussel *Mytilus edulis*. Conversely, Kowalewski (2004) found no consistent drill-hole stereotypy for *Nucella lamellosa* drilling the mussel *Mytilus trossulus*. This disagreement may be the result of uncertainty surrounding the term stereotypy rather than true biological differences in predatory behavior. Dietl (2000) operationally defines stereotypy as a statistically significant deviation from a random distribution. This demonstrates only that all locations on the shell are not drilled equally. In his discussion of site selectivity Kowalewski (2002) states that many predators are "behaviorally stereotyped in showing a preference for a particular location for their attack." Neither Dietl (2000) nor Kowalewski (2004) show convincing evidence of a preference by *Nucella* to drill a particular site, though both draw different conclusions regarding drill-hole stereotypy, and there is a large amount of variation in drill-hole position in both cases. Furthermore, Kowalewski (2004) shows large-scale variation in drill-hole site selection between multiple kills from a single gastropod individual. In this study, we will use the term drill-hole stereotypy to mean a preference for drilling a particular region of the prey shell. To evaluate stereotypy, we will employ a new operational definition using a sample's standard deviation (derived from the distance of each drill-hole from the mean drill-hole location for that sample).

This operational distinction is important, because drill-hole site selectivity ranges along a spectrum from a completely random distribution (where all portions of the shell drilled equally) at one end to a highly stereotyped, narrow distribution of drill-holes focusing on a particular anatomical region or structure (e.g., muscle tissue) at the other. A method commonly used to test for deviations from a random distribution involves arbitrarily dividing the shell into sectors, counting the number of drill-holes in each sector, and comparing the proportion of drill-holes in each sector with the proportion of shell comprising that sector (Kowalewski, 2002). There are a couple of limitations to this approach. First, the sectors may or may not have biologically meaningful boundaries and changes in the sector configuration or number of sectors may affect the outcome of the analysis. This is especially true in analyses with small sample sizes such as those found in experimental studies due to constraints of time and tank size. The second limitation of the sector method is that a non-random distribution in which all portions of the shell are drilled but are drilled with unequal frequency and a highly stereotyped case where drilling is focused on one anatomical feature cannot be discriminated from each other statistically, though they are substantially different in terms of their biological significance. By analyzing drill-hole stereotypy using the standard deviation of drill-hole placement, investigators define drill-hole placement using anatomically homologous landmarks or pseudo-landmarks, allow relative comparisons of stereotypy in multiple samples along temporal or spatial gradients, and are able to test quantitatively for differences in stereotypy by calculating confidence intervals. Standard deviation analysis does not allow one to test a single sample for the presence or absence of stereotypy, but it can easily be combined with a sector approach where necessary (Kowalewski, 2002). This strategy is easily combined with additional quantitative morphometric in order to test for differences in mean drill-hole placement (e.g., Canonical Variates Analysis) and retains information about the placement of individual drill-holes (e.g., for visual comparisons).

Drill-hole stereotypy is typically attributed solely to predator behavior (Kitchell, 1986; Kowalewski, 2002), but it may be influenced by prey behavior. For instance, clumping behavior in the mussel *Mytilus trossulus* may impact the prey handling/grappling capabilities or strategies of *Nucella* by restricting access to the shell surface. Kowalewski's (2004) experimental design failed to account for these potential effects as individual mussels were supplied to gastropods. The second aim of this study is to evaluate the effects of prey clumping on drill-hole stereotypy using geometric morphometric methods.

Materials and Methods

Specimen Collection:

Specimens of *Nucella lamellosa* (Gmelin 1791) and *Mytilus trossulus* (Gould 1850) were collected from the rocky intertidal of False Bay, San Juan Island, Washington, USA (Fig. Ap. 2) where both species are abundant. False Bay is an elongate semi-circular bay surrounded by rocky outcrop with large isolated boulders throughout. Boulders are separated by muddy and fine-grained sand substrate. False Bay is completely exposed during low tide and nearly submerged at high tide. *Nucella* specimens were collected from the rock wall at the south-southeast edge of the bay (the lower intertidal zone), and *Mytilus* specimens were collected from throughout the high and low intertidal zones including the rock wall and various boulders. Specimens were collected to include a full range of available sizes for both *Nucella lamellosa* and *Mytilus trossulus*. In the field, drilled mussel shells are very rare as barnacles are the preferred prey of *Nucella lamellosa* in this location (Hart and Palmer, 1987; Kowalewski, 2004), thus during our collection, we found only six drilled mussels.

Experimental design:

Mytilus shells were cleaned in the lab to remove encrusters in an effort to minimize the effect of encrustation on site selection of drilling gastropods. Each *Nucella lamellosa* specimen was measured to the nearest 0.01mm using a digital caliper and numbered prior to experimentation. Roughly 240 *Mytilus* and 87 *Nucella* were divided into two groups of equal numbers and size ranges and placed on opposite sides of a single sea table with running seawater. On one side (the individual mussel side), *Mytilus* specimens were evenly spaced and separated twice daily during the study interval to prevent clumping and minimize the number of gastropods found attached to mussels in pairs or groups (Fig.

Ap. 3a). Gastropods were allowed to hunt freely until they attached to a prey mussel at which point they were segregated from the rest with small, mesh cylinders to ensure a record of snail identity for each kill. Once the prey item was killed and abandoned, gastropods were released from the cage and again allowed to freely hunt. On the other side of the sea table (the clump side), *Mytilus* specimens were arranged into 13 piles (containing between 5 and 14 mussels) evenly spaced throughout the sea table and given a full day to attach to one-another using byssus threads (Fig. Ap. 3b) before gastropods were released. Gastropod movement was charted twice daily throughout the study interval to keep track of predator identity for each kill. Drilling gastropods were not caged on the clumped mussel side, so as not to prevent simultaneous attacks on mussels within the same clump. *Nucella lamellosa* specimens were starved for five days before the start of the experiment. All gastropods were returned to their original field location after the completion of the experimental period.

Shells of killed mussels were collected, examined for drill-holes, measured to the nearest 0.01mm using a digital caliper, and digitally imaged. Caliper measurements included maximum anterior-posterior length (length) and maximum dorsal-ventral length (width). Digital images were imported into ImageJ freeware and Cartesian x-y coordinates were collected for analysis of drill-hole placement in conjunction with four pseudo-landmarks: 1) anterior-ventral shell end, 2) anterior-dorsal flexure point, 3) maximum curvature of the posterior margin, and 4) posterior-ventral flexure point (Fig. Ap. 4A) after Kowalewski (2004). Pseudo-landmarks 1 and 4 were used as the baseline for Bookstein (shape) coordinate analysis (Bookstein, 1991). The digital images of all drilled left valves were mirrored before landmark collection to make them comparable with right valves. A randomly selected shell was selected for ten replicate analyses in an effort to estimate operator error (Fig. Ap. 4B).

Statistical analysis:

Differences in drilling frequency (number of successfully drilled mussels/total number of mussels present in treatment*100) were tested using two-tailed Fischer's Exact Test. Differences in mean drill-hole placement were tested using Canonical Variate Analysis. Differences in the variation of drill-hole placement were assessed by computing bootstrap

95% confidence intervals around standard deviation of both the x and y coordinates from both experimental treatments. In order to assess the effect of clump size on drilling frequency, clump-specific drilling frequency (number of successfully drilled mussels within a clump/total number of mussels present in clump*100) was plotted against clump size and a linear regression analysis was conducted on the resulting distribution. If gastropods are deterred by larger clumps, then the percent of mussels drilled should decrease with increasing clump size resulting in a negative correlation. All statistical analyses were conducted using SAS version 9.1 with SAS/IML codes written by M. Kowalewski. Alpha equals 0.05 for all tests.

Results

Gastropods did not show a preference for drilling right versus left valves regardless of clumping (Fisher's Exact Test, Two-sided Probability P = 0.61). Individual mussels frequently attached themselves to their nearest neighbors and required manual separation three times or more daily to prevent the formation of clumps. Both individual mussels and mussel clumps attached themselves to gastropods using byssus threads. Often the gastropod pulled the mussel(s) from their original location to the other side of the sea table and even up the side of the sea table walls. *Nucella* was never directly observed in the act of pulling mussels or mussel clumps but were found at rest on the sea table walls with mussels dangling from the back of their shells. The *Nucella* that experienced byssus attachment, which they could not dislodge, frequently suspended foraging and climbed above the water line. It is therefore unlikely that the gastropods moved the mussels in order to feed on them. This prey movement behavior is likely to be an artifact of the experimental setup as byssus attachment by mussels in naturally occurring clumps (which are much larger and more firmly adhered to hard substrates) would result in the pinning or trapping of gastropods (Day *et al.*, 1991). The byssus attachment to the gastropod shell is obviously very strong as the weight of 5-10 mussels suspended from the threads did not result in the snail's release.

Drilling frequency:

Drilling frequency is significantly different for the clumped mussels (28.1% of specimens drilled, n = 120) than for the individual mussels (45.7% of specimens drilled, n = 123) (Fischer's Exact Test, Two-sided Probability, P = 0.0063). Also, of 32 drilled clumped mussels, only two were recovered from the center of the clump and 30 from the margin of the clump. Drilling frequency within a clump is not significantly correlated with the number of mussels originally in the clump (Fig. Ap. 5) (Linear Regression, $R^2 = 0.13$, P = 0.20).

Drill-hole stereotypy:

Mean drill-hole location (Fig. Ap. 6A) is not significantly different in clumped mussels versus individual mussels (Canonical Variate Analysis, F = 0.67, P = 0.68). Variation in hole placement, as measured by variance, is not substantially different for clumped versus individual prey. Bootstrap 95% confidence intervals surrounding the variance values show considerable overlap (Fig. Ap. 6B). Drill-holes appear to be concentrated on the dorsal half to two-thirds of the shell within the pallial line.

Discussion

The effects of clumping behavior on drill-hole placement and stereotypy:

When reconstructing the record of fossil predator-prey interactions, paleontologists must rely on the types of physical evidence retained within fossil shells. Drill-hole placement and drill-hole stereotypy are commonly used to infer predator behavior (Kitchell, 1986). In fact aspects of both predator and prey behavior could conceivably influence drill-hole placement. In this study, we examined the potential effect of prey behavior, specifically clumping, on drill-hole site selection and stereotypy. Contrary to our predictions, clumping appears to have no effect on drill-hole site-selection neither in terms of anatomical location nor the amount of variation of sites selected (drill-hole stereotypy). There are two plausible explanations for this result. First, the tendency for gastropods to drill individuals at the outer rim of the clump may allow the gastropods equal access to all points on the outward facing valve. The second possibility is that differences in orientation of individual mussels within the clump between the experimental and natural clumps influence the results (refer back to Fig. Ap.1).

These alternative explanations could be tested by looking at the drill-hole stereotypy (or lack thereof) in natural aggregations of mussels. The lack of a prominent stereotypic pattern in the natural setting would support the first explanation and imply that the comparison of clumping and non-aggregating prey taxa in fossils is not a cause for concern (at least not when comparing mussels to other non-clumping taxa). The presence or absence of drill-hole stereotypy could be interpreted as a function of predatory behavior rather than the clumping behavior of the prey. If, however, natural populations show a higher degree of drill-hole stereotypy, one would have to be extremely cautious when inferring changes in predator behavior or predator identity when comparing drill-hole stereotypy data from a mix of clumping and non-clumping prey taxa. For example, a stereotypic pattern of drill-hole placement in clumped mussels and a non-stereotypic pattern of drill-hole placement in a solitary prey taxa from the same or similar environments may or may not indicate the presence of multiple drilling predators or a change in predatory behavior.

Evolutionary implications of clumping behavior as an anti-predatory strategy:

Although there are many slightly different techniques for calculating drilling frequency, all of them are meant to provide estimates of predation intensity. Predation intensity has been used to address questions about temporal patterns in predator-prey systems and has often been conducted on multiple prey taxa. Physiological differences (resulting in the difference in calorific value) have been taken into consideration when explaining difference in drilling frequencies in different taxa. Kitchell *et al.* (1981) showed that prey selection by extant naticids is consistent with predictions of cost-benefit analysis. Here we discussed yet another factor that might influence drilling frequency, namely clumping of prey.

The present study clearly indicates that clumping can reduce drilling frequency and thus may represent an effective anti-predatory strategy. One of two mechanisms may be responsible: 1) drilling predators avoid mussels in clumps because they represent dangerous prey whereas individual mussels do not, or 2) it is hard to reach mussels in the center of a clump allowing gastropods to prey only on individuals around the outside edge. A previous study by Day *et al.* (1991) showed that clumps of mussels can attach themselves to drilling predator with their byssus threads thereby pinning the gastropods in place and causing them to starve. Such evidence suggests that mussels constitute dangerous prey when clumped. Day *et al.* (1991) also observed that the mussels attach themselves more frequently to drilling gastropods than to herbivorous gastropods. In our study mussels attached themselves to the gastropods whether they were clumped or not, but in no instance did this appear to restrict gastropod movement. However, the largest clump in this study contained only 14 mussels making all clumps in this experiment small when compared to natural clumps (which can obtain a circumference as large as 5.2m (Harger, 1968)). We are therefore unable to test Day's suggestion because the effect on gastropod movement may require larger clumps than observed in the experiment. Data from the current experiment support mechanism 2: in 30 of 32 cases, drilled mussels came from the outside edge of the clump.

Further tests of the two mechanisms are possible. For example, if mechanism 1 is true, drilling gastropods might avoid bigger clumps, which are more dangerous than small clumps and individuals. We initially thought this might be the case given the experimental observation that gastropods sensed if a clump of mussels was attached to their shell and frequently abandoned foraging and moved out of the water in that situation. However, avoidance of large clumps should result in a negative correlation between drilling frequency and clump size. The current experiment yields the opposite pattern with a slightly positive correlation between drilling frequency and clump size. This evidence is far from conclusive since the range of clump sizes was narrow. A test of the prediction of mechanism 2, that there is an advantage to being located on the inside of a clump, would be to compare byssate and non-byssate taxa: even in the absence of byssul threads, clumping should result in lower drilling frequencies. While the experimental clumping of non-byssate taxa may not yield results relevant to natural systems where the clumping of non-byssate taxa is rare, it would allow one to tease apart the subtle differences between the hypothesized mechanisms proposed above.

Nucella's preference to feed on mussels located on the outside edge of clumps may have important evolutionary implications for aggregated individuals. The protection afforded to mussels living in clumps is highest in the center where the reproductive costs associated with an aggregated lifestyle are highest. This pattern holds true for both drilling predators as demonstrated in this study and crushing predators (Bertness and Grosholz, 1985; Okamura, 1986). A mussel living in the center of a clump, therefore, receives two separate anti-predatory benefits. In addition, aggregated living protects individual mussels from dislodgement by winter ice scour (Bertness and Grosholz, 1985) and other physical factors like desiccation (Seed, 1969). The complex interplay of metabolic costs with a multitude of benefits afforded to mussels by an aggregated lifestyle may make estimates of individual fitness more difficult. However, these revised estimates of individual fitness may eliminate the need to invoke higher order selection to explain the evolutionary advantage of an aggregated lifestyle. Okamura (1986) made a distinction between the selection which acts on groups of genetically identical clones versus the higher order selection which he felt must act on aggregated groups of individuals (such as mussels). Okamura's (1986) statements imply that individual selection could not account for the advent of an aggregated lifestyle in mussels and some type of group or species selection must be at work to surmount individual disadvantages such as reduced growth rate and decreased fecundity. A more complete picture of the numerous and varied benefits supplied by an aggregated lifestyle (as protection against multiple types and species of predators as well as different environmental variables) may reveal the selective advantage of living in clumps at the individual level.

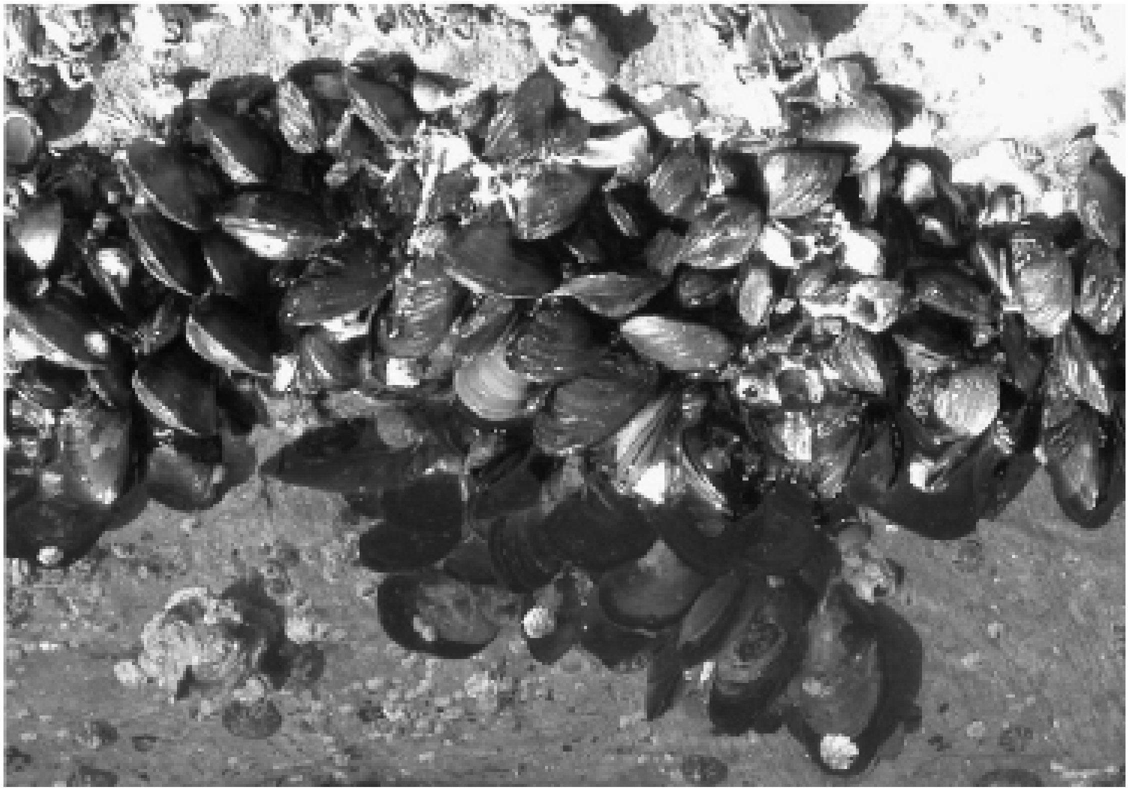

Fig. Ap.1. A natural aggregation of mussels from the rocky intertidal of Washington state. The preferred orientation of individuals is with the anterior-posterior axis perpendicular to the rock surface. Photo by J. Stempien.

Fig.Ap.2. Map of the study area showing (A) Washington with the location of San Juan Island highlighted within black box and (B) larger map of San Juan Island highlighting the location of False Bay.

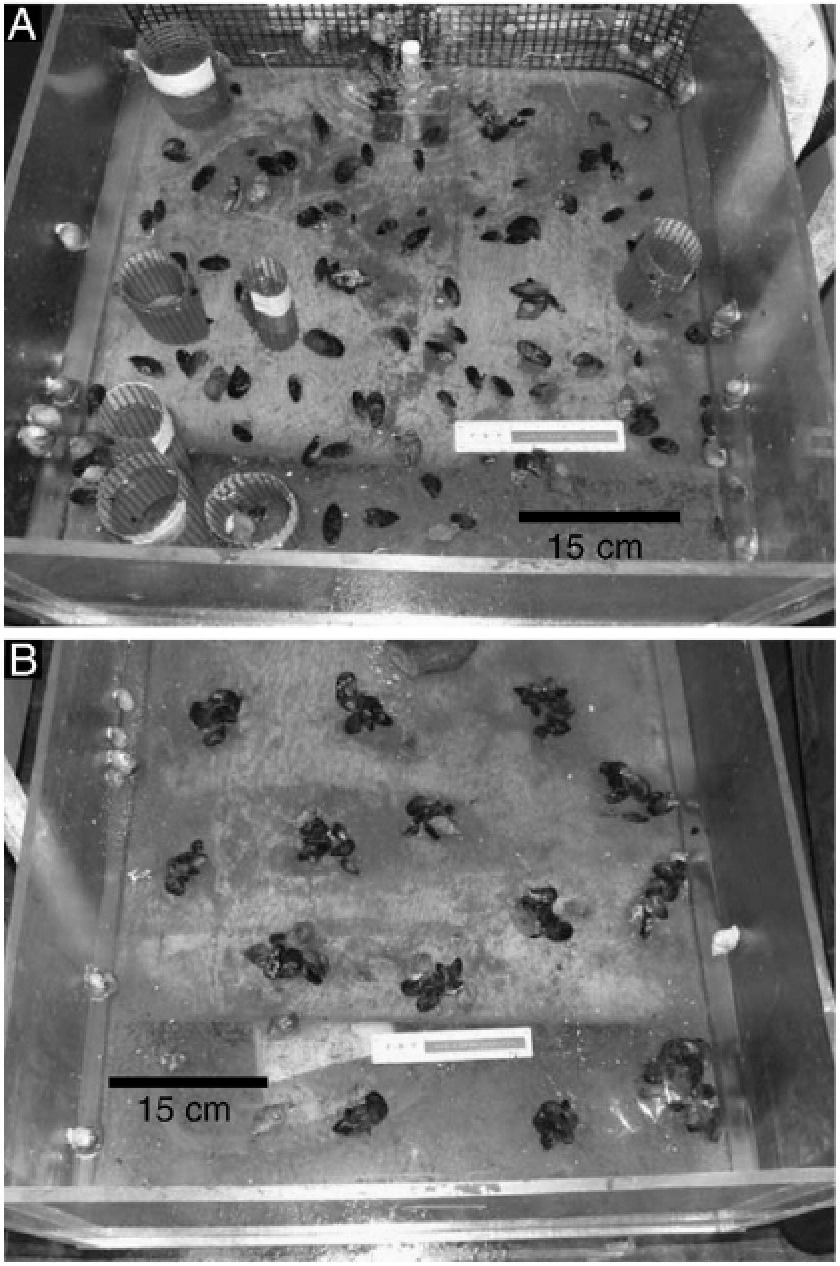

Fig. Ap.3. Photograph of the experimental set-up showing a sea table containing (A) the individual mussels and (B) the clumped mussels.

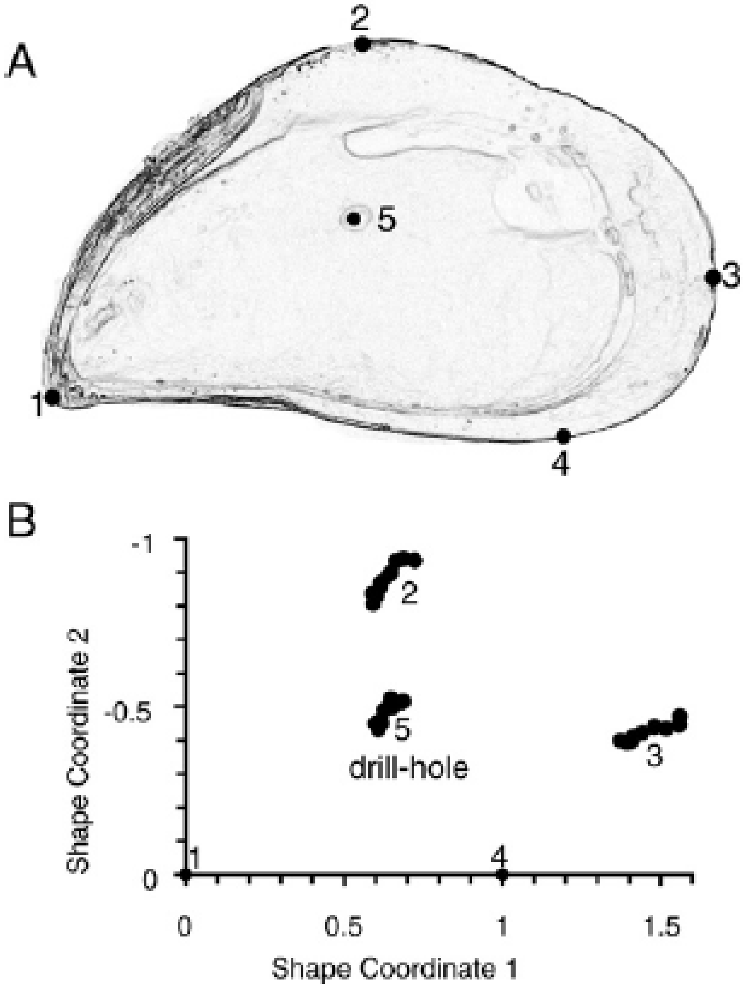

Fig. Ap. 4. A. Positions of the four pseudo-landmarks used for Bookstein analysis. Pseudo-landmarks 1 and 4 were used to designate the baseline. B. Bookstein plot of a single specimen photographed and digitized ten times to approximate operator error. The spread of points from a single landmark is minimal compared to distance between landmarks.

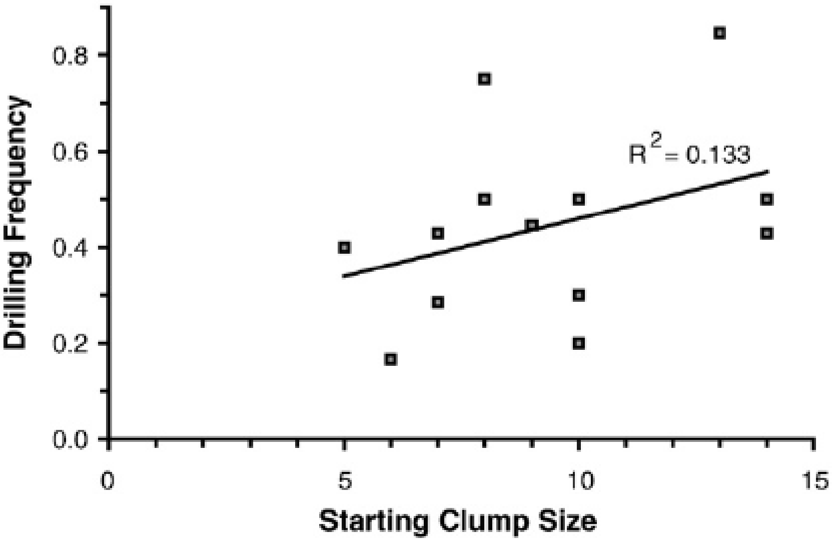

Fig. Ap.5. Clump-specific drilling frequency plotted against clump size. Variables are not significantly correlated $R^2 = 0.13$, $P = 0.20$.

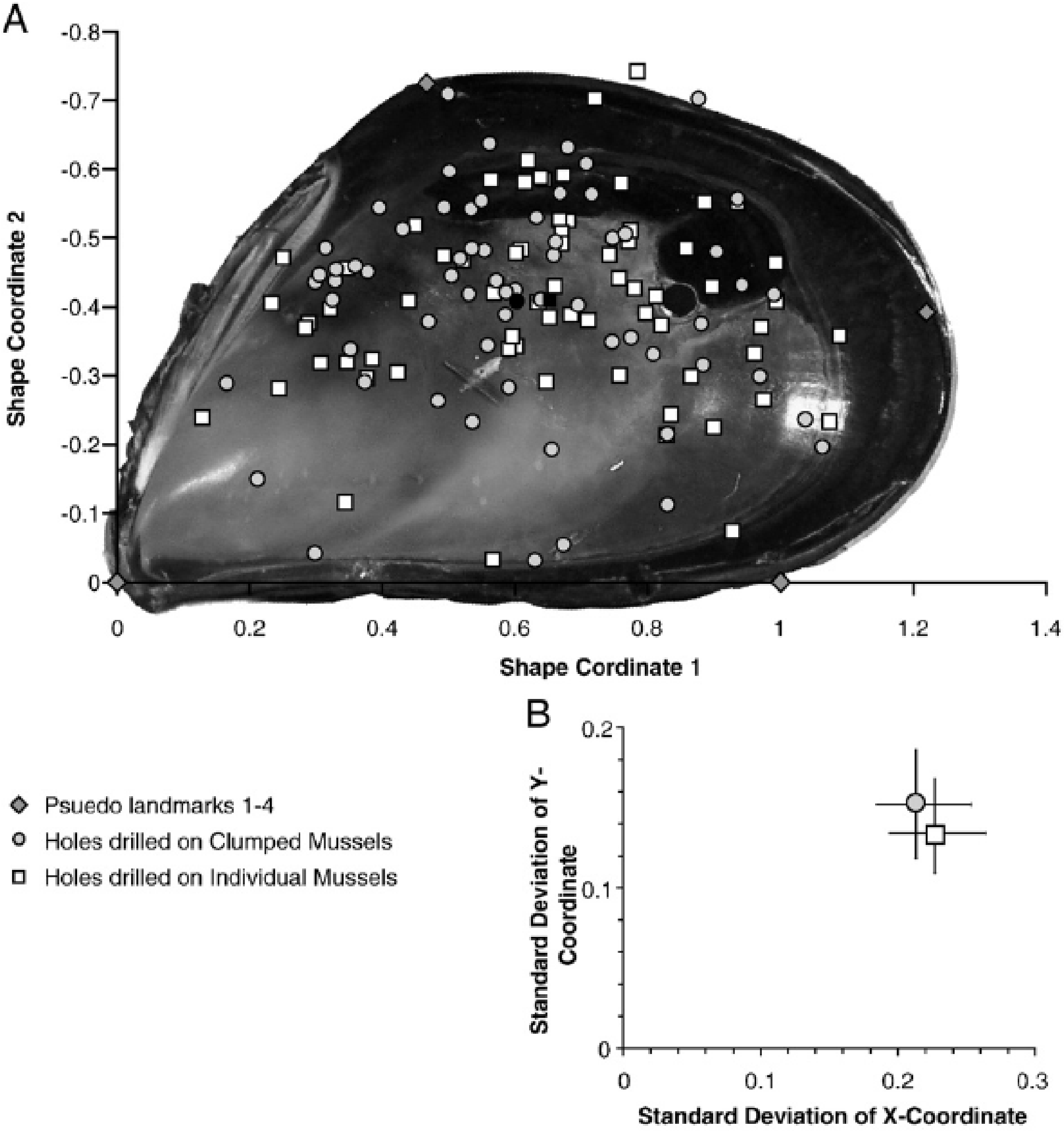

Fig. Ap.6. A. Bookstein plot showing drill-hole locations on individual specimens (white squares) and clumped specimens (gray circles) as well as the mean drill-hole location for all individual specimens (black square) and all clumped individuals (black circle). B. Variance in drill-hole placement for clumped (gray circles) versus individual (white squares) specimens with 95% bootstrap confidence intervals.

BIBLIOGRAPHY

Abrams, P. A., Menge, B. A., Mittlebach, G. G., Spiller, D. and Yodzis, P. 1996, The role of indirect effects in food webs, *in* G. Polis and K. Winemiller, eds., Food webs: dynamics and structure. Chapman and Hall, New York, New York, p. 371-395.

Alexander, R.R., 1975, Phenotypic lability of the brachiopod Rafinesquina alternata (Ordovician) and its correlation with the sedimentologic regime: Journal of Paleontology, v. 49, p. 607-610

Alexander, R.R., 1984, Comparative hydrodynamic stability of brachiopod shells on current-scoured arenaceous substrates: Lethaia, v. 17, p. 17-32.

Alexander, R. R. and Dietl, G. P., 2001, Shell repair frequencies in New Jersey bivalves: a recent baseline for tests of escalation with Tertiary, Mid-Atlantic congeners: Palaios, v.16, p. 354-371.

Alexander, R. R. and Dietl, G. P., 2003, The fossil record of shell-breaking predation on marine bivalves and gastropods, *in* Kelley, P.H., Kowalewski, M., Hansen, T.A., eds., Predator–Prey Interactions in the Fossil Record: Topics in Geobiology Series 20. Plenum Press/ Kluwer, New York, pp. 141–170.

Allmon, W. D., Nieh, J. C. and Norris, R. D., 1990, Drilling and peeling of Turritelline gastropods since the Late Cretaceous: Palaeontology, v. 33, p. 595-611.

Amano, K., 2006, Temporal pattern of naticid predation on *Glycymeris yessoensis* (sowerby) during the Late Cenozoic in Japan: Palaios, v. 21**,** p.369-375.

Anderson, L.C., 1992, Naticid gastropod predation on corbulid bivalves: Effects of physical factors, morphological features and statistical artifacts: Palaios, v. 7, p. 602-617.

Anderson, L. C., Geary, D. H., Nehm, R. H. and Allmon, W. D., 1991, A comparative study of naticid gastropod predation on *Varicorbula caloosae* and *Chione cancella*, Plio-Pleistocene of Florida,U.S.A: Palaeogeography, Palaeoclimatology, Palaeoecoiogy, v. 85, p. 29-46.

Andrews E.A., 1935, Shell repair by the snail, Neritina: Journal of Experimental Zoology, v. 70, p. 75–107.

Ansell, A.D., 1960, Observations on predation of *Venus striatula* (Da Costa) by *Natica alderi* (Forbes): Proceedings of the Malacological Society of London, v.34, p. 248-249.

Ansell, A.D., Morton, B., 1987, Alternative predation tactics of a tropical naticid gastropod: Journal of Experimental Marine Biology and Ecology, v.111, p.109-119.

Aronson, R. B. and Blake, D. B., 2001, Global Climate Change and the Origin of Modern Benthic Communities in Antarctica: American Zoologist, v. 41, p.27–39.

Arua, I. and Haque, M., 1989, Predatory gastropod boreholes in an Eocene molluscan assemblage from Nigeria: Lethia, v. 22, p. 49-52

Atema, J. and Burd, G.D., 1975, A field study of chemotactic responses of the marine mud snail *Nassarius obsoletus*. Journal of Chemical Ecology, v.1, p. 243–251.

Ausich, W. I. and Gurrola, R. A., 1979, Two boring organisms in a Lower Mississippian community of southern Indiana: Journal of Paleontology, v. 53, p. 335-344.

Ballinger R.E., 1979, Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona: Ecology, v. 60, p. 901–909.

Bambach, R., 1993, Seafood through time: Changes in biomass, energeticsand productivity in the marine ecosystem: Paleobiology, v. 19, p. 372-397.

Baumiller, T. K. 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods: Palaeontology, v. 33, p. 743-748.

Baumiller, T. K. and Bitner, M. A., 2004, A case of intense predatory drilling of brachiopods from the Middle Miocene of southeastern Poland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 214, p. 85-95.

Bayne, B. L. and Schullard, C., 1978a, Rates of oxygen consumption by *Thais (Nucella) lapillus* (L.): Journal of Experimental Marine Biology and Ecology, v.32, p. 97-111.

Bayne, B. L. and Schullard, C., 1978b, Rates of feeding by *Thais (Nucella) lapillus* (L.): Journal of Experimental Marine Biology and Ecology, v. 32, p. 113-129.

Behrens, E.W. and Watson, R. L., 1969, Differential sorting of pelecypod valves in the swash zone: Journal of Sedimentary Petrology, v. 39, p. 159-165.

Berg, C, J, Jr. and Nishenko, S., 1975, Stereotypy of Predatory Boring Behavior of Pleistocene Naticid Gastropods: Paleobiology, v.1, p. 258-260.

Bertness, M. D. and Grosholz, E., 1985: Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of a clumped distribution: Oecologia, v. 67, p. 192–204.

Bookstein, F.L., 1991, Morphometric tools for landmark data. Cambridge University

Press, New York.

Bottjer, D., 1985, Bivalve paleoecology, *in* D. J. Bottjer, C. S. Hickman and P.D. Ward, eds., Mollusks: Notes for a short course, University of Tennessee, Department of Geological Sciences Studies in Geology, v. 13, pp. 112-137.

Boucot, A. J., 1953, Life and death assemblages among fossils. American Journal of Science, v. 251, p. 25-40.

Boucot, A.J., Brace, W. and Demar, R., 1958, Distribution of brachiopod and pelecypod shells by currents: Journal of Sedimentary Petrology, v. 28, p. 321–332.

Brenchlev, P.I. and Newall, G., 1970, Flume experiments on the orientation and transport of models and shell valves: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 7, p. 185220.

Burrows, M. T. and Hughes, R. N., 1991, Optimal foraging decisions by dogwhelks, *Nucella lapillus* (L.): Influences of mortality risk and rate-constrained digestion: Functional Ecology, v. 5, p. 461-475.

Calvet, C., 1992, Borehole site-selection in *Naticarius hebraeus* (Chemnitz in karsten, 1769) (Naticidae: Gastropoda)?: Orsis, v. 7, p. 57-64.

Carriker, M. R. and Van Zandt, D., 1972a, Regeneration of the accessory boring organ of muricid gastropods after excision: Transaction of American Microscopical Society, v. 91, p. 455-466.

Carriker, M. R. and Van Zandt, D., 1972b, Predatory behavior of a shell-boring Muricid gastropod. *In* H. E. Winn and B. L. Olla, eds., Behavior of Marine Animals: current perspective in research, v. 1, p. 157-242

Carriker, M. R. and Yochelson, E. L., 1968, Recent gastropod boreholes and Ordovician cylindrical borings: United States Geological Survey Professional Paper 593-B, p. 1-26.

Casey, M. and Chattopadhyay, D., 2008, Clumping behavior: an anti-predatory strategy against drilling predation: Journal of Experimental Marine Biology and Ecology, v. 367, p. 174-179.

Chattopadhyay, D. and Baumiller, T. K., 2007, Drilling under threat: An experimental assessment of the drilling behavior of Nucella lamellosa in the presence of a predator: Journal of Experimental Marine Biology and Ecology, v. 352, p. 257-266.

Chattopadhyay, D. and Baumiller, T. K., 2008, Effect of durophagy on drilling predation: Geological Society of America Abstracts with Programs, Vol. 40, No. 8, p. 208

Christensen, B. A., 1981, On the risk of erosion of cohesionless sea floors: Oceans, v. 13, p. 706-714.

Colbath, S. L., 1985, Gastropod Predation and Depositional Environments of Two Molluscan Communities from the Miocene Astoria Formation at Beverly Beach State Park, Oregon: Journal of Paleontology, v. 59, p.849-869.

Conway morris, S. and Bengtson, S., 1998, Cambrian Predators: Possible Evidence from Boreholes: Journal of Paleontology, v. 68, p. 1-23.

Côté, I. M., 1995, Effects of predatory crap effluent on byssus production in mussels: Journal of Experimental Marine Biology and Ecology, v. 188, p. 233-241.

Côté, I. M. and Jelnikar, E., 1999, Predator-induced clumping behaviour in mussels (*Mytilus edulis* Linnaeus): Journal of Experimental Marine Biology and Ecology, v. 235, p. 201-211.

Day, R.W., Barkai, A. and Wickens, P. A., 1991, Trapping of three drilling whelks by two species of mussel: Journal of Experimental Marine Biology and Ecology, v. 149, p. 109-122.

Dayton, P. K., 1990, Polar benthos, *in* W. O. Smith, Jr., ed., Polar oceanography, Part B: Chemistry, biologyand geology, Academic Press, San Diego, pp. 631-685

De Cauwer, G., 1985. Gastropod predation on corbulid bivalves—Palaeoecology or taphonomy?: Annales de la Socie´te´ Royale Zoologique de Belgique, v. 115, p. 183–196.

Deline, B., Baumiller, T., Kaplan, P., Kowalewski, M. and Hoffmeister, A., 2003, Edge-drilling on the brachiopod *Perditocardinia cf. P. dubia* from the Mississippian of Missouri (USA): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 201, p.211-219.

Dey, S., 2003, Incipient motion of bivalve shells on sand beds under flowing water: Journal of Engineering Mechanics. DOI: 10.1061/(ASCE)0733-9399(2003)129:2(232)

Dietl, G.P., 2000, Successful and unsuccessful predation of the gastropod *Nucella lapillus* (Muricidae) on the mussel *Mytilus edulis* from Main: Veliger, v. 43, p. 319-329.

Dietl, G. P. and Kelley, P. H., 2002, The Fossil Record of Predator-Prey Arms Races: Coevolution and Escalation Hypotheses: Paleontological Society Papers, v. 8, p. 353-374

Dietl, G.P. and Kelley, P.H., 2004, Emergent effects of multiple predators on prey in the fossil record: Geological Society of America Abstracts with Programs, v. 36, p. 480

Dietl, G. P., Alexander, R. R. and Bien, W., 2000, Escalation in Late Cretaceous–early Paleocene oysters (*Gryphaeidae*) from the Atlantic Coastal Plain: Paleobiology, v. 26, p. 215-237.

Dietl, G. P. and Alexander, R. R., 1998, Shell repair frequencies in whelk and moon snails from Delaware and southern New Jersey: Malacologia, v. 39, p.151-165.

Dietl, G. P. and Alexander, R. R., 2000, Post-Miocene shift in stereotypic Naticid predation on confamilial prey from the Mid-Atlantic shelf: coevolution with dangerous prey: Palios, v. 4, p.414–429.

Dietl, G. P. and Herbert, G.S., 2002, Experiments with the predatory muricid *Chicoreus dilectus* and its bivalve prey *Chione elevata*: Does edge drilling decrease prey handling time?: American Malacological Society Abstract, p.44

Dietl, G.P., Alexander, R.R., 1995, Borehole site and prey size stereotypy in naticid predation on *Euspira (Lunatia) heros* Say and *Neverita (Polinices) duplicate* Say from the southern New Jersey coast: Journal of Shellfish Research, v.14, p. 307-314.

Dill, L. M., 1987, Animal decision making and its ecological consequences: the future of aquatic ecology and behavior: Canadian Journal of Zoology, v. 65, p. 803–811.

Dudley, E. C. and Vermeij, G. J., 1978, Predation in time and space; drilling in the gastropod Turritella: Paleobiology, v.4, p. 436-441.

Ellers, O. 1995, Form and motion of *Donax variabilis* in flow: Biological Bulletin, v. 189, p.138-147.

Farrell, U. C. 2004. The effect of salinity changes on the predation of *Nucella lamellosa* on *Mytilus trossulus.* Project report-Predator-prey interactions (Zoology-533), Friday Harbor Laboratories, University of Washington. 67.

Frey, R. W. and Dörjes, G., 1988, Fair and foul-weather shell accumulations on a Georgia beach: Palaios, v. 3, p. 561-576.

Frey, R. W. and Henderson, S. W., 1987, Left-right phenomena among bivalve shells: examples from the Georgia coast: Senckenbergiana maritima, v. 19, p. 223-247.

Futerer, E., 1982, Experiments on the distinction of wave and current influenced shell accumulations, *in* Seilacher. A., ed., Cyclic and Event Stratification: Berlin, Springer-Verlag, p. 175-179

Gmelin, J.F., 1791, Carli Linnaei systema Naturae per regna tria naturae: Editio decimatertia, aucta, reformata, Vermes Testacea Leipzig [Lipsiae], v.1, p. 3021-3910

Gould, S. J., 1985, The paradox of the first tier: an agenda for paleobiology: Paleobiology, v.11, p. 2-12.

Gutiérrez, R.M. and Gallardo, C.S 1999, Prey attack, food preference and growth in juveniles of the edible muricid snail, *Chorus giganteus* : Aquaculture, v. 174, p. 69-79.

Hagadorn, J. and Boyajian, G. E., 1997, Subtle changes in mature predator-prey systems; an example from Neogene Turritella (Gastropoda): Palios, v. 4, p. 372-379.

Hagstrom, K. M., 1996, Effects of compaction and wave-induced forces on the preservation and macroevolutionary perception on Naticid predator-prey interactions. Unpublished M.S. Thesis. Indiana University.

Hanks, J.E., 1957, The rate of feeding of the common oyster drill, *Urosalpinx cinerea* (say), at controlled water temperatures: Biological Bulletin, v.112, p. 330-335.

Hansen, T. A. and Kelley, P. H., 1995, Spatial variation of naticid gastropod predation in the Eocene of North America: Palios, v. 10, p. 268-278.

Harger, J.R.E., 1968, The role of behavioral traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*: Veliger, v.11, p. 45-49.

Harper, E. M. and Skelton, P. W., 1993, The Mesozoic marine revolution and epifaunal bivalves: Scripta Geologica, Special issue v.2, p. 127-153.

Harper, E. M., 2006, Dissecting post-Palaeozoic arms races: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 232, p. 322– 343

Harper, E. M., Forsythe, G. T. W. and Palmer, T, 1998, Taphonomy and the Mesozoic Marine Revolution: preservation state masks the importance of boring predators: Palios, v. 13, p. 352-360.

Hart, M.W. and Palmer, A.R., 1987, Stereotypy, ontogenyand heritability of drill site selection in thaidid gastropods: Journal of Experimental Marine Biology and Ecology, v. 107, p. 101-120.

Hjülstrom, F., 1939, Transportation of detritus by moving water, Part I, Transportation. *In* Trask, P.D. ed., Recent Marine Sediments; A Symposium: Tulsa, Oklahoma, American Association of Petroleum Geologists. p. 5-31

Hoffman, A. and Martinell, J., 1984, Prey selection by gastropods in the Pliocene of Emporda (Northeast Spain): Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 7, p. 393-399.

Hoffman, A., 1976, Mortality patterns of some bivalves from the Badenian (Miocene)

Korytnica Clays, Poland, Neues Jahrbuch fur Geologie tind Paliiontologie: Monatshefte, v. 1976, p. 337-349.

Hoffman, A., Pisera, A.and Ryszkiewicz, M., 1974, Predation by muricid and naticid gastropods on the Lower Tortonian mollusks from the Korytnica Clays: Acta Geologica Polonica, v. 24, p. 249-260.

Hoffmeister, A. P. and Kowalewski, M., 2001, Spatial and Environmental Variation in the Fossil Record of Drilling Predation: A Case Study from the Miocene of Central Europe: Palios, v. 16, p. 566-579.

Hughes, R. N. and Dunkin, S. B., 1984, Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory: Journal of Experimental Marine Biology and Ecology, v. 77, p. 45-68.

Huntley, J. H. and Kowalewski, M., 2007, Strong coupling of predation intensity and diversity in the Phanerozoic fossil record: Proceedings of the National Academy of Sciences, v.104, p. 15006–15010.

Jablonski, D. and Sepkoski, J. J. Jr., 1996, Paleobiology, community ecologyand scales of ecological pattern: Ecology, v. 77, p.1367-78.

Johnson, R. G., 1958, Experiments on the burial of shells: Journal of Geology, v. 65, p. 527-535.

Jonkers, H. A., 2000, Gastropod predation patterns in Pliocene and Recent pectinid bivalves from Antarctica and New Zealand: New Zealand Journal of Geology and Geophysics, v. 43, p. 247-254.

Kabat, A. R. and Kohn, A. J., 1986, Predation on Early Pleistocene naticid gastropods in Fiji: Paleogeography, Paleoclimatology, Paleoecology, v. 53, p. 255-269.

Kabat, M. R., 1990, Predatory ecology of naticid gastropods with a review of shell boring predation: Malacologia, v. 32, p. 155-193.

Kardon, G., 1998, Evidence from the fossil record of an antipredatory exaptation: conchiolin layers in corbulid bivalves: Evolution, v. 52, p. 68-79.

Kelley, P.H., 1989, Evolutionary trends within bivalve prey of Chesapeake Group naticid gastropods: Historical Biology, v.2, p. 139-156.

Kelley, P.H., 1991, The effect of predation intensity on rate of evolution of five Miocene bivalves: Historical Biology, v. 5, p.65-88.

Kelley, P. H. and Hansen, T. A., 1996: Recovery of naticid gastropod predator-prey system from the Cretaceous-Tertiary and Eocene-Oligocene extinctions: Geological

Society Special Publication, v.102, p. 373-386

Kelley, P. H. and Hansen, T. A., 2001, The role of ecological interactions in the in the evolution of Naticid gastropods and their molluscan prey. *In* Allmon, W., David J Bottjer, D. J., eds., Evolutionary Paleoecology: The Ecological Context of Macroevolutionary Change. Columbia University Press, New York, pp. 149-170

Kelley, P. H. and Hansen, T. A., 2003, The fossil record of drilling predation on bivalves and Gastropods. *In* Kelley, P. H., Kowalewski, M. and Hansen, T. A., eds., Predator-Prey Interactions in the Fossil Record: Topics in Geobiology Series 20, Plenum Press/Kluwer, New York, pp. 113-133

Kelley, P. H., Thomann, C., Hansen, T. A., Aronson, R. and Blake, D., 1997, A world apart but not so different: predation by naticid gastropods in Antarctica and the U. S. Gulf Coast during Eocene: Geological Society of America Abstract with Programs, v. 29, p. A107.

Kent, B.W., 1981, The behavior of the gastropod *Amphissa columbiana* (Prosobranchia: Columbellidae): Veliger, v. 23, p. 275-276

Kitchell, J. A., Boggs, C. H., Kitchell, J. F. and Rice, J. A., 1981, Prey selection by Naticid gastropods: experimental tests and application to the Fossil record: Paleobiology, v. 7, p. 533-552.

Kitchell, J. A., 1986, The evolution of predator-prey behavior: naticid gastropods and their molluscan prey. *In* Nitecki, M.H., ed., Evolution of Animal Behavior: Paleontological and Field Approaches. Oxford University Press, Cary, NC, pp. 88-110

Konicker, L. S., Wise, C. D. and Wise, J. M., 1963, Factors affecting the distribution of opposing mollusk valves: Journal of Sedimentary Petrology, v. 33, p. 703-712.

Kontrovitch, M., 1975, A study of the differential transportation of ostracodes: Journal of Paleontology, v. 49, p. 937-941.

Kontrovitch, M. and Snyder, S. W., 1981, Reliability of microfossil assemblages as paleoenvironmental indicators: Transections-Gulf Coast Association of Geological Societies. v. 31, p. 323-324

Kontrovitch, M., Snyder, S. W. and Brown, R. J., 1978, A flume study of the movement of the foraminifera tests: Paleogeography, Paleoclimetology, Paleoecology, v. 23, p. 141-150.

Kowalewski, M., 1993, Morphometric analysis of predatory drill-holes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 102, p. 69-88.

Kowalewski, M., 2002, The fossil record of predation: an overview of analytical methods: Paleontological Society Special Papers, v. 8, p. 3-42.

Kowalewski, M., 2004, Drill holes produced by the predatory gastropod *Nucella lamellosa* (Muricidae): paleobiological and ecological implications: Journal of Molluscan Studies, v. 70, p. 359–370.

Kowalewski, M., Dulai, A. and Fuersich, F. T., 1998, A fossil record full of holes; the Phanerozoic history of drilling predation: Geology, v. 26, p. 1091-1094.

Krebs, J., 1977, Optimal foraging: theory and experiment: Nature, v. 168, p. 583-584

Labarbera, M., 1977, Brachiopod orientation to water movement: Theory, laboratory behavior and field orientations: Paleobiology, v. 3, p. 270-287.

Leighton, L. R., 2001, New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success: Palaeogeography, Palaeoclimatology, Palaeoecology, v.165, p. 53–69.

Leighton, L. R., 2002, Inferring predation intensity in the marine fossil record: Paleobiology, v. 28, p. 328–342.

Leighton, L. R., 2003, Morphological response of prey to drilling predation in the Middle Devonian: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 201, p. 221-234.

Lever, J., 1958, Quantitative beach research I. The “left-right phenomenon”: sorting of lamellibranch valves on sandy beaches: Basteria, v. 22, p. 21-51.

Lever, J. and Thijssen, R., 1968, Sorting phenomena during the transport of shell valves on sandy beaches studied with the use of artificial valves: *In* Fretter, V., ed., Studies in the Structure, Physiologyand Ecology of Molluscs: Symposia of the Zoological Society of London, v. 22, p. 259–271.

Lever, J., Kessler, A., Van Over Beeke, P.and Thijssen, R, 1961, Quantitative beach research II, The "hole effect": A second mode of sorting of lamellibranch valves on sandy beaches: Netherlands Journal of Sea Research, v. 1, p. 339358.

Lima, S. L., 1988a, Nonlethal effects in the ecology of predator–prey interactions—what are the ecological effects of prey interactions—what are the ecological effects of anti-predator decision making?: BioScience, v. 48, p. 25–34.

Lima, S. L., 1988b, Stress and decision making under the risk of predation: recent developments from behavioral, reproductiveand ecological perspectives: Advances in the Study of Behavior, v. 27, p. 215–290.

Lima, S.L. and Dill, L.M., 1990, Behavioral decisions made under the risk of predation:

a review and prospectus: Canadian Journal of Zoology, v. 68, p. 619–640.

Lin, J., 1991, Predator-prey interactions between blue crabs and ribbed mussels living in clumps: Estuarine and Coastal Shelf Science, v. 32, p. 61-69.

Madin, J. S., Alroy, J., Aberhan, M. and Fursich, F. T., 2006, Statistical Independence of escalatory ecological trends in phanerozoic marine invertebrates: Science, v. 314, p. 925.

Madin, J. S., Alroy, J., Aberhan, M. and Fursich, F. T., 2008, Response to Comments on "Statistical Independence of Escalatory Ecological Trends in Phanerozoic Marine Invertebrates": Science, v. 312, p. 897.

Manhart, M., 1998, Vortex shedding from a hemisphere in a turbulent boundary layer: Theoretical and Computational Fluid Dynamics, v. 12, p. 1–28.

Manzi, J. J., 1970, Combined effect of salinity and temperatureon the feeding, reproductiveand survival rates of *Eupleura caudata* (Say) (Prosobranchia: Muricidae): Biological Bulletin, v.138, p. 35-46.

Marko, P. B. and Palmer, A. R., 1991, Responses of a rocky shore gastropod to the effluents of predatory and non-predatory crabs: avoidance and attraction: Biological Bulletin, v. 181, p. 363–370.

Martin-Kaye, P., 1951, Sorting of lamellibranch valves on beaches in Trinidad: B.W.I. Geological Magazine, v. 88, p. 432-434.

McKlitrick, M.A., 1987. Experiments on the settling of gastropod and bivalve shells: biostratinomic implications, *In* Flessa, K.W. ed. Paleoecology and Taphonomy of Recent to Pleistocene Intertidal Deposits, Gulf of California: Paleontological Society, Special Publication 2, p. 150-163.

Menard, H.W. and Boucot. A. J., 1951, Experiments on the movement of shells by water: American Journal of Science, v. 249, p. 131-151

Messina, C. and Labarbera, M., 2004, Hydrodynamic behavior of brachiopod shells: experimental estimates and field observations: Palaios, v. 4, p. 441-450.

Miller, D. J., 1991, Hydrodynamic behavior of drilled and undrilled bivalve shells: Potential sources of taphonomic bias: Geological Society of America, Abstracts with Programs, v. 23, p. A458.

Moody, R. M. and Aronson, R. B., 2007, Trophic heterogeneity in salt marshes of the northern Gulf of Mexico: Marine ecology progress series, v. 331, p. 49–65.

Moran, M. J., 1985, Effects of prey density, prey size and predator size on rates of feeding by an intertidal predatory gastropod *Morula marginalba* Blainville (Muricidae), on several species of prey: Journal of Experimental Marine Biology and Ecology, v. 90, p. 97-105

Morton, B. and Chan, K., 1999, Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gastropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nassarius festivus* in Hong Kong: Journal of Experimental Marine Biology and Ecology, v. 240, p. 213-228.

Nagle, J. S., 1964, Differential sorting of shells in the swash zone: Biological Bulletin, v. 127, p. 353.

Nagle, J. S., 1967, Wave and current orientation of shells: Journal of Sedimentary Petrology, v. 37, p. 1124-1138.

Navarro, J. M., Leiva, G. E., Gallardo, C. S. and Varela, C., 2002, Influence of diet and temperature on physiological energetics of *Chorus giganteus* (Gastropoda: Muricidae) during reproductive conditioning: New Zealand Journal of Marine and Freshwater Research, v. 36, p. 321–332

Okamura, B., 1986, Group living and the effects of spatial position in aggregations of *Mylitus edulis*: Oecologia, v. 69, p. 341-347.

Olivera, A.M. and Wood, W. L., 1997, Hydrodynamics of bivalve shell entrainment and transport: Journal of Sedimentary Research, v. 67, p.514-526.

Palmer, A. R., 1990, Effect of crab effluent and scent of damaged conspecifics on feeding, growth and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.): Hydrobiologia, v. 193, p. 155–182.

Pieron, H., 1933, Notes éthologiques sur les Gastéropodes perceurs et leur comportement. Arch. d. Zool. expérimentate et générale. Second volume jubilaire.

Quaresma V. S., Amos, C. L. and Bastos, A. C., 2007, The influence of articulated and disarticulated cockle shells on the erosion of a cohesive bed: Journal of Coastal Research, v. 23, p. 1143-1451.

Rand, A. S., 1954, Variation and predation pressure in an island and a mainland population of lizards: Copeia, v. 1954, p. 260–262.

Rasband, W.S., 1997-2007. ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/

Reineck, H. E. and Singh, I. B., 1975, Depositional Sedimentary Environments: Published by Springer-Verlag. pp.549

Reyment, R. 1999, Drilling gastropods, *In* E. Savazzi, ed., Functional Morphology of invertebrate Skeleton, John Wiley and Sons, Ltd, pp. 197-204

Roopnarine, P. D. and Willard, S., 2001, Bivalve prey morphology as a guide to drilling stereotypy of Naticid and Muricid gastropods: venerids, naticids and muricids in Tropical America: PaleoBios, 21, v. 2, p. 109-110

Roopnarine, P. D. and Beussink, A., 1999, Extinction and naticid predation of the bivalve Chione Von Muhlfeld in the Late Neogene of Florida: Palaeontologica Electronica, v. 2, art. 1: 24 p., 719 kB.

Rovero, F., Hughes, R. N. and Chelazzi, G., 1999, Automatic recording of the radular activity of dogwhelks (*Nucella lapillus*) drilling mussels (*Mytilus edulis*): Journal of Marine Biology Association U.K., v. 79, p. 1079-1083

Roy, K., Miller, D. J., Labarbera, M, 1994, Taphonolic bias in analysis of drilling predation: effects of gastropod drill holes on bivalve shell strength: Palaios, v. 9, p. 413-421

SAS Institute, 2002-2003, Statistical Analytical Software-Interactive Matrix Language, Version 9.1.3: Cary, NC, USA.

Savarese, M., 1994, Taphonomic implications of flow-induced forces on concavo-convex articulate brachiopods: an experimental approach: Lethaia, v. 27, p. 301-312.

Savory, E and Toy, N., 1986, The flow regime in the turbulent near wake of a hemisphere: Experiments in Fluids, v. 4, p.181–188.

Schall, J. J. and Pianka, E. R., 1980, Evolution of escape behavior diversity: The American Naturalist, v. 115, p.551–566.

Seed, R., 1969, The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. I. Breeding and Settlement: Ocecologia, v. 3l, p. 277-316.

Shaffer, H. B., 1978, Relative predation pressure on salamanders (Caudata: Plethodontidae) along an altitudinal transect in Guatemala: Copeia, v. 1978, p. 268–272.

Signor, P. W. III and Brett, C. E., 1984, The Mid-Paleozoic Precursor to the Mesozoic Marine Revolution: Paleobiology, v. 10, p. 229-245.

Sih, A., Crowley, P., Mcpeek, M., Petranka, J. and Strohmeier, K., 1985, Predation, competition and prey communities: a review of field experiments: Annual Review of Ecology and Systematic, v. 16, p. 269–311.

Sih, A., Englund, G. and Wooster, D., 1998, Emergent impacts of multiple predators on prey: Trends in Ecology and Evolution, v. 13, p. 350–355.

Sohl, N. F., 1969, The Fossil Record of Shell Boring by Snails: American Zoologist, v. 9, p. 725-734.

Stanley, S. M., 1974, Effects of competition on rates of evolution, with special reference to bivalve mollusks and mammals: Systematic Zoology, v. 22, p. 486-506.

Stanley, S. M., 1976, Fossil data and the Precambrian-Cambrian evolutionary transition: American Journal of Science, v. 276, p. 56-76.

Stanton Jr., R. J. and Nelson, P. C., 1980, Reconstruction of the trophic web in paleontology: community structure in the Stone City Formation (middle Eocene, Texas): Journal of Paleontology, v. 54, p. 118–135.

Statzner, B. and Holm, T. F., 1989, Morphological adaptation of shape to flow: Microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions: Oecologia, v. 78, p. 145-157.

Steer, M. A. and Semmens, J. M., 2003, Pulling or drilling, does size or species matter? An experimental study of prey handling in *Octopus dierythraeus* (Norman, 1992): Journal of Experimental Marine Biology and Ecology, v. 290, p. 165-178

Stenzler, D. and Atema, J., 1977, Alarm response of the marine mud snail *Nassarius obsoletus*: specificity and behavioral priority: Journal of Chemical Ecology, v. 3, p. 159–172.

Stump, T. E., 1975, Pleistocene molluscan paleoecology and community structure of the Puerto Libertad region, Sonora, Mexico: Paleogeography, Paleoclimatology, Paleoecology, v.17, p. 177-226

Taylor, J. D., Cleevly, R. J. and Morris, N. J., 1983, Predatory gastropods and their activities in the Blackdown Greensand (Albian) England: Palaeontology, v. 26, p. 521-553.

Taylor, J. D., 1970, Feeding habits of predatory gastropods in a Tertiary (Eocene) molluscan assemblage from the Paris basin: Palaeontology, v. 23, p. 254-260.

Taylor, J. D., Morris, N. J.and Taylor, C. N., 1980, Food specialization and the evolution of prosobranch gastropods: Palaeontology, v. 26, p. 521-553.

Taylor, J. D. and Morton, B., 1996, The diets of predatory gastropods in the Cape d'Aguilar Marine Reserve, Hong Kong: Asian Marine Biology, v. 13, p. 141-166

Thomas, M. and Day, R. W., 1995, Site selection by a small drilling predator: why does the gastropod *Haustrum baileyanum* drill over muscle tissue of the abalone *Haliotis rubra*? Marine and Freshwater Research, v. 46, p. 647-655.

Trewin, N. H. and Welsh, W., 1972, Transport, breakage and sorting of the bivalve *Maetra corollina* on Aberdeen Beach, Scotland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 12, p. 193-204.

Trussell, G. C, Patrick, E. J. and Bertness, M. D., 2003, Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates: Ecology, v. 84, p. 629-640.

Tull, D. S. and Bohning-gaese, K., 1993, Patterns of Drilling Predation on Gastropods of the Family Turritellidae in the Gulf of California: Paleobiology, v. 19, p. 476-486.

Turner, A. M., 1996, Freshwater snails alter habitat use in response to predation: Animal Behavior, v. 51, p. 747–756.

Turner, A. M. and Mittlebach, G. G., 1990, Predation avoidance and community structure: interactions among piscivores, planktivoresand plankton: Ecology, v. 71, p. 2241–2254.

Turner, A. M., 1997, Contrasting short-term and long-term effects of predation risk on consumer habitat use and resources: Behavioral Ecology, v. 8, p. 120–125.

Turner, A. M., Bernot, R. J. and Boes, C. M., 2000, Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails: Oikos, v. 88, p. 148–158.

Turner, A. M., Fetterolf, S. A. and Bernot, R. J., 1999, Predator identity and consumer behavior: differential effects of fish and crayfish on the habitat use of a freshwater snail: Oecologia, v. 118, p. 242–247.

Urrutia, G. X. and Navarro, J. M., 2001, Patterns of shell penetration by *Chorus giganteus* juveniles (Gastropoda: Muricidae) on the mussel *Semimytilus algosus*: Journal of Experimental Marine Biology and Ecology, v. 258, p. 141-153.

Velbel, M. A. and Brandt, D. S., 1989, Differential preservation of brachiopod valves: Taphonomic bias in *Platystrophia ponderosa*: Palaios, v. 4, p. 193–195.

Vermeij, G. J., 1980, Drilling predation of bivalves in Guam: some paleoecological implications: Malacologia, v. 19, p. 329-334

Vermeij G. J., 1982, Unsuccessful predation and evolution: The American Naturalist, v.120, p. 701–720.

Vermeij, G. J., 1983, Traces and trends of predation, with special reference to bivalved animals: Palaeontology, v. 26, p. 455-465.

Vermeij, G. J., 1987, Evolution and escalation: An ecological history of life, Princeton University Press, Princeton, NJ, 527pp.

Vermeij, G. J., 1994, The evolutionary interaction among species: selection, escalation and coevolution: Annual Review of Ecology and Systematics, v. 25, p. 219-236.

Vermeij, G. J., 2002, Evolution in the consumer age: Predators and the history of life. *In* Kowalewski, M. and Kelley, P. H., eds., The fossil record of predation: Paleontological Society Special Papers, v. 8, p.375-393. Yale University, New Haven.

Vermeij, G. J. and Dudley, E. C, 1982, Shell repair and drilling in some gastropods from the Ripley Formation (Upper Cretaceous) of Southeastern U.S.A.: Cretaceous Research, v. 3, p. 397-403

Vermeij, G. J. and Carlson, S. J., 2000, The muricid gastropod subfamily Rapaninae: phylogeny and ecological history: Paleobiology, v. 26, p. 19-46

Vermeij, G. J., Zipser, E. and Dudley, E. C., 1989, Successful and unsuccessful drilling predation in Recent pelecypods: Veliger, v. 32, p. 266-273

Vignali, R. and Galleni, L., 1986, Naticid predation on soft bottom bivalves: a study on a beach shell assemblage: Oebalia, v. 13, p. 157-178

Vogel, S. and Labarbera, M., 1978, Simple flow tanks for research and teaching: Bioscience, v. 28, p. 638–643.

Walker, S. E., 2001, Paleoecology of gastropods preserved in turbiditic slope deposits from the Upper Pliocene of Ecuador: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 166, p. 141-163.

Werner, E. E. and Anholt, B. R., 1993, Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity: American Naturalist, v. 142, p. 242–272.

Wilbur, H. M. and Fauth, J. E., 1990, Experimental aquatic food webs: interactions between two predators and two prey: American Naturalist, v. 135, p. 176–204.

Wooton, J. T., 1994, Predicting direct and indirect effects: an integrated approach using experiments and path analysis: Ecology, v. 75, p. 151–165.

Ziegelmeir, E., 1954, Beobachtungen fiber den Nahrungserwerb bei der Naticide Lunatia nitida Donovan (Gastropoda Prosobranchia): Helgolander Wissenschaftliche Meeresforschung, v. 5, p. 1-3

Zlotnik, M., 2001, Size-related changes in predatory behaviour of naticid gastropods from Middle Miocene Korytnica Clays, Poland: Acta Palaeontologica Polonica, v. 46,

p. 87-97.

Zuschin, M. and Stanton, R. J. Jr., 2001, Experimental Measurement of Shell Strength and its Taphonomic Interpretation: Palaios, v.16, p.161-170.