**University of Alberta**

# Using Drilled-Undrilled Shell Damage Analysis to Estimate Crushing Predation Frequencies in Modern Marine Gastropod Assemblages

by

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# ABSTRACT

Predation is a frequently studied subject, but estimating crushing predation in mollusk communities is challenging. Shells record successful attacks, but it is not always possible to identify attacks on an individual basis. Repair scar frequency is a common proxy for crushing mortality, but shell repair does not directly measure mortality, so results are ambiguous. Borrowing a technique from Vermeij (1982), crushing mortality frequencies were estimated in a recent shell assemblage. Because crushing damage can be confused with taphonomy, a taphonomic baseline was established: the cause of death of drilled shells is known, so additional damage is postmortem. The frequencies of several damage types were tallied for drilled shells to estimate a taphonomic baseline for the assemblage. The same frequencies were calculated for undrilled shells (cause of death unknown). In many cases, undrilled shells had significantly higher frequencies than drilled shells. The differences in damage frequencies likely are caused by crushing predation.

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# 1. INTRODUCTION

## *1.1. Quantifying Crushing Predation*

While the importance of crushing predation as a major influence on the evolution and ecology of marine mollusks is well recognized (Vermeij 1977, Vermeij 1987), relatively few techniques permit crushing predation to be quantified. Direct observation of predation is difficult in modern environments and impossible in the fossil record, so it is necessary to develop proxies— other measurable variables that in some way reflect true crushing predation rates. Shell repair frequency has emerged as a common proxy for crushing predation (Vermeij et al. 1980, Vermeij et al. 1981, West et al., 1991, Alexander and Dietl 2001), as repair scars are typically the only easily identifiable evidence of predatory attack (Vermeij et al. 1981). A shell may have one or more repair scars, each indicating an attempted, but failed, predatory attack. Repair frequency (the number of repair scars per total population or the number of repaired individuals per total population) often is assumed to be a valid proxy for attack frequency and for predation intensity (the frequency of prey mortality due to crushing predation). Populations with higher repair frequencies are assumed to have accordingly higher predation mortality than populations with lower repair frequencies (Alexander and Dietl 2003). For this to be true, both failed and successful predation must increase relative to non-predatory mortality as a result of increasing attack frequency. In other words, attack frequency (the proportion of the prey population that is attacked) increases, while the success frequency (the proportion of attacked prey that are killed) stays the same, resulting in a higher repair frequency. For example, this could occur if the predator population increased but the predators’ crushing ability stayed the same. However, this is not the only way to increase the repair frequency: a decrease in predator strength relative to the prey’s ability to defend itself (with no change in the predator population size), or an increase in prey defense with no concomitant change in predation intensity, would result in a decreased success rate. Repair frequency increases because a higher percentage of attacked prey survives to repair the damage. While the direction of change in repair frequency is the same in both scenarios, the prey mortality (the percentage of prey killed by predation) is very different: predatory mortality increases in the first scenario, but decreases in the second scenario (Vermeij 1987; Leighton 2002) (Figure 1). Thus, repair frequency alone is not a reliable indicator of predation pressure on a prey population.

Because of the problems with shell repair as a proxy, estimates of crushing predation intensity should be derived from data representing actual kills, rather than the survivors of predation attempts. Direct observation of crushing predation can be logistically difficult or impossible, especially when the aim is to gather enough data to calculate predation mortality. Another potential proxy for predation intensity is the diversity or absolute abundance of crushing predators in the system. However, the effects of increased predator abundance on prey populations are not necessarily direct or easily predictable (Menge 1978, Menge 1995) and increased predator diversity can intensify (Byrnes et al. 2006) or relieve predation pressure on prey populations (Finke and Denno 2004, Siddon and Witman 2004). Even if the relationships between predator abundance, diversity, and predation pressure were certain, examination of such relationships in the fossil record is extremely difficult due to poor preservation and the uncertain identity of predators (see Leighton 2002 and references therein). Tethering and caging experiments have also been used to estimate predation mortality in modern environments (Ray and Stoner 1995, Behrens Yamada and Boulding 1996, Boulding et al. 1998, Rochette and Dill 2000), but such techniques may operate on too small of a scale to capture predator-prey dynamics over large geographic and temporal ranges.

Because of the problems associated with the above techniques for measuring predation, trace evidence from the crushed shells may be the best proxy for predation mortality. Crushing predators can leave highly characteristic and recognizable evidence of their attack, such as the wedge-shaped trace created when a crab peels into a gastropod’s shell aperture. In many cases, however, it is difficult to distinguish between damage caused by crushing predation and damage due to transportation, compaction, or other post-mortem factors. Thus, counting only shells bearing characteristic damage attributed to crushing predation probably underestimates the true rate of crushing predation mortality, whereas counting all shells bearing any damage almost certainly overestimates crushing predation.

Vermeij (1982) bypassed this problem of identifying individual instances of damage due to crushing predation by using the damage on drilled shells to calculate a baseline taphonomic damage frequency for a whole shell population.

Shell drilling is employed by certain groups of predatory gastropods to kill their shelled prey (often other gastropods). After the prey is consumed, its shell is left with a distinctive, often highly stereotyped, borehole. The presence of this complete hole through an empty gastropod shell indicates that the individual was killed by a drilling gastropod, not a crushing predator. Thus, any other unrepaired damage to the shell (chips, cracks, or holes) occurred post-mortem and is of taphonomic origin. Drilled and undrilled shells from the same gastropod population likely experience the same taphonomic conditions and thus should have equal frequencies of taphonomic damage (Figure 2). If the undrilled shell population has a higher frequency of total damage, the difference between this total damage frequency and the baseline taphonomic damage frequency represents the frequency of damage caused by crushing predation (Figure 3). This method, of estimating the frequency of damage due to predation by calculating a taphonomic baseline from drilled shells, is herein referred to as Drilled-Undrilled Shell Damage Analysis (DUSDA).

While certain caveats must be considered (see Discussion), the benefit of this method is that, unlike repair frequency, interpretation of the results is unambiguous: the technique estimates crushing frequency based on unrepaired damage to the shell, which is directly proportional to predation mortality. Repair scars, on the other hand, result from unsuccessful attacks, whose relationship with actual predatory mortality is uncertain.

Because DUSDA does not require live gastropods, its use does not depend on favorable tides and weather the way *in situ* monitoring of marine communities does. Large amounts of material can be gathered quickly and as frequently as needed, and can be analyzed in the laboratory or the field. The technique is also not limited to modern environments; drilled mollusks have a deep fossil history, so this method has great potential for use in the fossil record. By allowing ecologists and paleontologists to measure crushing predation frequency of mollusk populations more accurately, this approach has broad implications for the study of how ecology influences evolution in predator-prey systems.

### *1.2. Crushing Predation on Gastropod Mollusks*

Predation may be one of the most important influences on the evolution of life and the ecology of living systems, but it is still a relatively poorly understood process, demanding the attention of paleontologists and ecologists alike. Predation in the marine realm, in particular, may have been responsible for some of the most important innovations in the history of life; one example may be the advent of hard skeletons in animals (Vermeij 1989). Gastropod mollusks, most of which bear shells, are one of the most successful groups of animals alive today and are useful for studying predator-prey systems, as various gastropod taxa may be prey (e.g., Vermeij 1982, Ray and Stoner 1995, Behrens Yamada and Boulding 1998, Rochette and Dill 2005), predators (e.g., Delance and Emig 2004, Grey et al. 2005), or both (e.g., Kelley 1991). In addition to being diverse and abundant in modern environments, gastropods have a deep and rich fossil record (Wagner 1995, Jablonski and Roy 2003), which gives scientists opportunities to understand the relationship between durophagy and defensive skeletons.

Durophagous predators are any organisms that consume hard-shelled prey (Vermeij 1977). This includes predators that ingest their prey whole, pry open shells, drill through shells, and crush shells. Whole ingestion and prying rarely leave easily recognizable evidence, but drillers and crushers, which include some of the most important predators of gastropods, always do damage to the shell. Predation on mollusks has a long history. Paleozoic durophages included groups of mollusks and arthropods; however, the durophagous abilities of Paleozoic predators were minor compared with later taxa (Walker and Brett 2002). Many of these groups suffered or were completely eliminated in the end-Permian extinction. The Mesozoic Era saw the appearance of what are now the most abundant and diverse groups of crushing predators: brachyuran crabs, stomatopod crustaceans, teleost fishes, and rays (Walker and Brett 2002). The Mesozoic Marine Revolution (MMR) (Vermeij 1977) also included the appearances of higher vertebrate durophages such as birds and giant marine reptiles. The MMR was actually a series of radiations that continued into the Cenozoic, despite the loss of some groups at the end-Cretaceous extinction (e.g., marine reptiles). In fact, some groups that appeared during the Mesozoic experienced dramatic radiations in the Cenozoic, including brachyuran crabs and teleost fishes (Walker and Brett 2002).

Durophagous crustaceans, especially brachyuran crabs, are diverse and abundant in marine ecosystems and are among the most important invertebrate shell crushers. Crabs employ varied methods of attack (Zipser and Vermeij 1978). One method is to attempt to crush the shell outright by grabbing the whole shell within the chela and crushing. If the crab is successful, the shell is probably broken into many pieces and it may be difficult to distinguish these pieces from a shell broken by non-predatory means (e.g., crushed by debris or during transport). If the outright crush is not practical (if, for example, the snail is too large), the crab may attempt to chip or peel the shell from the outer apertural margin. The crab grasps the shell with one chela, inserts the dactyl or the fixed finger of the other chela into the aperture of the shell, and chips away pieces of the shell until it reaches the flesh of the snail, which has retracted into the shell behind its operculum. The crab can then pull out the flesh. After the initial peeling, the crab does little damage to the shell beyond minor abrasion caused by cleaning the shell of all traces of flesh. Thus, the empty shell is left with a signature, wedge-shaped indentation that starts at the aperture and points back into the body whorl (Figure 4). If a predator is interrupted during peeling, the snail may survive and repair the shell, leaving a distinctive trace (Vermeij and Dudley 1982). Unlike outright crushing, the damage caused by successful and unsuccessful peeling can be identified. It has been observed in modern laboratory settings (Bertness and Cunningham 1981, West et al. 1991, Donovan et al. 1999) and has been documented in the fossil record (e.g., Vermeij et al. 1980, Allmon et al. 1990). Peeling is nevertheless more destructive than predatory drilling, and “messier” instances of peeling conceivably can be confused with taphonomic damage, whereas naticid-type boreholes are never caused by taphonomic means. (See “4.1 Non-predatory Causes of Damage to Gastropod Shells,” below.)

### *1.3. Drilling Predation versus Crushing Predation*

Crushing and drilling predation are two types of durophagous predation that leave traces on the prey shell. The two most important groups of modern predatory drillers are gastropods in the families Naticidae (the moon snails) and Muricidae (murex snails or rock snails, sometimes also erroneously referred to as whelks). Drilling predation has been studied extensively not just because it is ecologically important to prey populations but also because predatory boreholes are easy to identify in the fossil record (Dudley and Vermeij 1978). Predatory boreholes are almost always circular in plan-view, are oriented perpendicular to the prey shell surface (the most direct path to prey soft tissues), and are often stereotypic in their location, occurring on a particular region of the prey shell (Carriker and Yochelson 1968, Leighton 2001). Naticid boreholes, in particular, have a distinctive beveled edge (conical in cross-section), making them easy to identify (Figure 5). In this study, naticid predatory boreholes exhibited the expected stereotypy, tending to occur just outside the inner wall of the aperture. Complete predatory boreholes typically do not co-occur on prey shells, as the first complete borehole usually results in the death of the prey. In rare cases, a drilling predator may be interrupted after the hole is completed but before it can kill the prey, and it or another driller must start over and create a new hole; however, out of the 2,242 shells examined in this study, only one shell possessed two complete naticid boreholes. Incomplete boreholes are also found on live gastropods and empty shells (personal observation), indicating that a predator was interrupted before the hole could be completed. Individual gastropods may bear multiple incomplete boreholes.

The differences between drilling and crushing predation result in differences in preservation and identification of these attack traces in both modern and fossil shell deposits. The characteristic shape, orientation, and stereotyped location of predatory boreholes make it relatively easy to identify such holes and to calculate predatory drilling rates in modern and fossil shell deposits. Crushing predation, being more destructive to the shell, can be difficult or impossible to positively identify on individual shells or fragments. While the focus of this study was not on drilling predation, drilled shells were necessary for establishing the taphonomic baseline that allowed the estimation of crushing predation frequencies.

## 2. METHODS

### *2.1. Collection of Study Materials*

The modern dead gastropod shell assemblage used in this study was collected by Erin Pearson and Lindsey Leighton at Torrey Pines State Beach in Del Mar, California, USA (32º 52’ N, 117º 15’ W). The locality is a sandy beach with occasional low-relief exposures of the underlying sandstones and igneous rocks. Dense pockets of shell material and pebbles tend to collect on the beach after storms and near the mouth of Soledad Creek, an estuarine marsh.

Approximately three two-litre bags of sieved material (shells, intact and fragmented; pebbles; sand; and organic debris) were used in this study. The material was bulk-collected; that is, there was no selection for certain taxa or for well-preserved or intact specimens. The only biases present in the raw material relate to which taxa and which particles happened to collect in the shell pockets. This may be controlled by the local abundance of taxa and by fluid-particle interactions that carried and deposited the particles (Lever et al. 1961, Albertzart and Wilkinson 1990). Despite the potential for these factors to bias the sample, the raw material contained a wide diversity of shells, suggesting that the sample was representative of the overall gastropod community.

The most abundant taxon in the sample was *Olivella biplicata* (Family Olivellidae), the purple dwarf olive snail (Figure 6a). Specimens ranged from 8.1 to 23.9 mm tall with an unornamented, relatively thick shell.

The next most abundant taxon was *Olivella beatica* (Family Olivellidae) the beatic dwarf olive snail (Figure 6b). *O. beatica* is smaller than *O. biplicata* (4.0 to 19.5 mm in length) and is taller relative to its circumference. *O. beatica* has an unornamented, relatively thick shell, though less thick than that of *O. biplicata*.

The third most abundant taxon was *Conus californicus* (Family Conidae), the California cone snail. These shells varied greatly in size, ranging from less than 5 mm to over 30 mm in length, and have unornamented, relatively thick shells.

The fourth most abundant taxon was the mud snail *Nassarius perpinguis* (Family Nassariidae), the western fat nassa (Figure 6c). This gastropod ranged in size from 8.6 to 22.8mm in length and has a relatively thin shell with basket weave-like ornament. *N. perpinguis* tended to be more poorly preserved than the thicker-shelled taxa.

The moon snail *Euspira* (formerly *Polinices*) *lewisii* (Family Naticidae) was also common in the sample (Figure 6d). The shells ranged in size from 4.2 to 41.9 mm in length and have unornamented, very thick shells.

Many other gastropod taxa were present in the sample, but in much lower abundances. These included members of the families: Epitoniidae (wentletraps), Triviidae (trivias, sometimes referred to as cowries), Terebridae (auger shells), Turritellidae (tower shells), Turridae, Trochidae (top shells), Lottiidae (true limpets), Fissurellidae (keyhole limpets), Haminoeidae (bubble snails), Vermetidae (worm shells), Calyptraeidae (slipper shells), and others. In addition to gastropods, the sample contained numerous bivalves and sparse crustacean, echinoderm, insect, and plant fragments.

Although *Euspira lewisii* was present in the material collected by Ms. Pearson, most of the *E. lewisii* material was collected by Lindsey Leighton and Chris Schneider at Torrey Pines State Beach. The material consisted solely of *E. lewisii*. All specimens bore either the apex or the upper (older) part of columella (in cases where the apex had been abraded or chipped off). While the collection of these *E. lewisii* was more discriminating than Ms. Pearson's collection, the shells still varied greatly in degree of damage. Because the collection criteria for this material was similar to the specimen-selection criteria (see "Selection of Study Specimens"), the material was deemed appropriate for the study.

### *2.2. Selection of Study Taxa*

The taxa used in this study were selected based on the following criteria:

1. Shells must be sufficiently abundant to achieve a reasonable sample size (at least 200 total specimens).

2. Shells must be identifiable to the species level. Because different species, even within a single genus, may inhabit slightly different habitats and experience different levels of predation, it cannot be assumed that similar species can be lumped together for the purposes of quantifying shell damage and estimating predation rates.

3. Drilled shells must be sufficiently abundant. The Drilled/Undrilled Shell Damage Analysis method requires drilled shells for the calculation of taphonomic baselines to which the undrilled shell damage frequencies are compared. The samples of the chosen taxa each comprised at least 100 drilled shells.

*Olivella biplicata, O. beatica, Nassarius perpinguis,* and *Euspira lewisii* met all three criteria and were included in the study. *Conus californicus* was abundant and identifiable, but because predatory drilling rates on the species were extremely low, there were not enough drilled shells to calculate the taphonomic baselines. *C. californicus* was not included in the study.

*Euspira lewisii* material from Ms. Pearson and Dr. Leighton’s collection was combined with *E. lewisii* collected by Drs. Leighton and Schneider to be used in this study.

No other gastropod taxa met the selection criteria, due to low abundances and/or low predatory drilling rates.

### *2.3. Selection of Study Specimens*

Not all specimens or fragments of each taxon could be used in the study. Study specimens were selected according to the following criteria. Because the shell morphology and characteristics varied among the taxa, the specifics of each criterion were adjusted for each taxon.

1. Individual shells must be counted in such a way that single snails cannot be counted twice. A shell landmark (a single, readily identifiable location or feature of the shell) was selected for each taxon. Only shells bearing this landmark were selected for the study. Landmark identification prevents double counting of individuals. For example, a snail shell may break into two pieces, one with the apex and one with the aperture. Unless a landmark is used, each piece can be counted, resulting in one individual being counted twice. If a landmark, for instance the apex, is used, no shell can be counted twice because no shell possesses two apices.

For *Olivella biplicata*, *O. beatica*, and *Nassarius perpinguis*, the shell apex was not a practical landmark, because the apex was commonly abraded or removed from the shell. The penultimate whorl (the whorl immediately above the ultimate, or body, whorl) was chosen as a landmark because it is a unique feature, it is easily distinguishable from the other whorls on full-grown specimens, and many shells possessed it (Figure 6a-c). Shells bearing at least 50% of the penultimate whorl were selected for the analysis.

*Euspira lewisii* is extremely low-spired (previous whorls are mostly covered by newer whorls), so the penultimate whorl was not a practical landmark. For *E. lewisii*, the point where the apertural margin and the whorl suture (line along which the newer whorls are in contact with older whorls) meet was chosen as the landmark (Figure 6d). When this landmark is not visible, much or all of the body whorl may have been removed from the shell.

Shells lacking their respective landmarks were excluded from the study.

2. It must be possible to confidently determine whether a shell bears (or might have borne) a predatory borehole. Shells that have been fragmented may be missing material that did bear a predatory borehole. In fact, the area of shell that bears a borehole may be weakened and more prone to damage than other areas of the shell (Roy et al. 1994). Fortunately, naticid boreholes are often highly stereotyped in their location on the prey shell. On intact shells in the present study, the holes rarely occurred outside of the inner margin of the aperture. Shells that were missing a significant amount of material in this area (enough that it was impossible to tell whether there was a borehole) were not included in the analysis. Most *O. biplicata*, *O. beatica*, and *E. lewisii* shells that met the previous criteria also met this criterion. *N. perpinguis* shells, however, often were missing this area and had to be discarded, resulting in lower sample sizes relative to the actual abundance.

All of the shell material from Torrey Pines State Beach was sorted and all usable specimens (meeting the above criteria) were collected for each taxon (see Table 1).

### *2.4. Drilled-Undrilled Shell Damage Analysis*

After all shells were collected that met the above criteria, the chosen shells were divided into drilled and undrilled groups. The drilled groups consisted of shells bearing naticid predatory boreholes, which were identified based on the following criteria: holes were large (>1mm), circular in plan-view, oriented perpendicular to the shell surface, and conical in cross-section. Muricid boreholes are more difficult to identify: they are smaller and cylindrical in cross-section (Carriker and Yochelson 1968), so they can be confused with non-predatory borings. Potential muricid borings were also infrequent in the study assemblages; muricid-drilled shells were not used to determine the taphonomic baseline in the study.

The frequencies of several types of damage were recorded for both the drilled and undrilled samples of each species. The types of damage recorded were chosen to represent variation in location, extent, and nature of the damage. The categories were *not* chosen to represent damage probably caused by crushing predators, because this would necessitate subjective judgments on the origin of damage and could bias the results.

1. Apex damage: Damage to the apex was divided into two subcategories according to severity:

*a. apex abrasion*: the apex is worn, but upper whorls have not necessarily been removed (Figure 7b)

*b. apex removal*: the upper whorls of the shell have been removed by fracture, not abrasion (Figure 7a)

2. Damage to shell aperture margin: Any damage (missing shell material) to the outer lip of the shell opening (where the living snail emerges from the shell) was further divided into subcategories encompassing a range of severity (Figure 7b-f). This category does not include cracks, where shell material was broken but no material was missing.

*a. aperture abrasion*: visible wear on aperture margin, but no visible shell breakage (Figure 7b)

*b. shallow aperture chip*: visible breakage to shell margin, but breakage does not significantly alter the shape of the margin (Figure 7c)

*c. deep aperture chip*: breakage and missing shell extends into the body whorl and alters the shape of the margin (Figure 7d)

*d. extensive aperture peeling*: damage to margin extends far into body whorl, but does not exceed half of the whorl (Figure 7e)

*e. major damage to the body whorl*: damage extends into body whorl so that at least half the body whorl material has been removed (Figure 7f)

Damage subcategories *b* and *c* were initially tallied separately for the adapical (closer to the apex) and abapical (farther from the apex) regions of the aperture margin. However, these were combined for the analysis because of the difficulty in confidently assigning a chip to either the adapical or abapical region.

3. Apertural cracks: These were cracks propagating from the aperture margin into the body whorl (shell material is broken, but no material is missing).

4. Cracks in body whorl: The body whorl (the youngest part of the shell, the portion occupied by the living snail) was cracked, but the crack does not originate in the aperture margin and no holes are present.

5. Holes in the body whorl: This includes any open holes in the body whorl except intact predatory boreholes or holes created by other boring organisms.

6. Columella damage: This is any damage to the columella (the spiral core of the shell), from chipping to complete removal (Figure 7f).

Three types of shell damage that could not be related to crushing predation were also measured to test the assumption that the drilled and undrilled groups of shells experience the same taphonomic forces.

7. Boring or pinhole drills: This includes any small holes that are oriented approximately perpendicular to the surface, but are not positively identifiable as naticid predatory boreholes. Pinhole drills could potentially include muricid boreholes, which are very small and cylindrical in cross-section. If pinhole drills are more frequent in undrilled shells, this may indicate that some of the pinholes are muricid predatory boreholes.

8. Extensive boring traces: The shell bears numerous pinholes and boring trails (not perpendicular to shell surface), which are attributable to boring organisms such as clionid sponges and spionid polychaetes that use the shell as living space (Figure 8).

9. Incomplete boreholes: The shell bears a mark that is identifiable as an attempted naticid borehole, but the hole does not penetrate the shell, indicating that that particular predation attempt was unsuccessful.

For each damage category, every specimen bearing the particular type of damage was counted. Any given specimen could bear multiple types of damage (see Figure 2), so individual shells could be counted for any number of damage categories. For the remainder of this discussion, “drilled shells” refers to shells with a complete bore hole. Drilled and undrilled shells were counted separately. The number of damaged shells (drilled or undrilled) was divided by the total shells (drilled or undrilled), resulting in damage frequencies for each damage category. For each damage category, the damage frequency of the drilled shells represents the taphonomic damage frequency. Each taxon had a set of damage frequencies that, taken together, describe typical taphonomic damage for that taxon.

The number of damaged undrilled shells was divided by the total number of undrilled shells, to calculate the damage frequency for each type of damage on undrilled shells. When the damage frequency of undrilled shells was higher than that of the drilled shells, the difference between the frequencies represents the minimum frequency of damage due to predation (see Figure 3 for example). For example, in a hypothetical population of shells, 26% of the drilled shells and 53% of the undrilled shells have columella damage. Applying the equation

$$\mathrm{Frag\%}_U - \mathrm{Frag\%}_D = \mathrm{Frag\%}_P$$

(where $\text{Frag\%}_U$ is the percent of undrilled shells that bear the type of damage in question, $\text{Frag\%}_D$ is the percent of drilled shells with that damage, and $\text{Frag\%}_P$ is the calculated percentage of shells where that damage is attributable to predation),

$$53\% - 26\% = 27\% = \text{Frag\%}_P$$

the percentage of shells with columella damage caused by predation is 27%.

The calculation of damage frequencies depends on the assumption that taphonomic conditions are similar between drilled and undrilled shells. Roy et al. (1994) found that drilled bivalve shells are more susceptible to taphonomic damage than undrilled shells. It is likely any such bias in the drilled gastropod assemblage would result in an overestimated taphonomic baseline (because the drilled shells would be in overall poorer condition than the undrilled shells) and a conservative estimate of the frequency of damage due to crushing. Furthermore, the calculated frequency of damage due to crushing ($\text{Frag\%}_P$) is conservative because crushing predation is by nature destructive. At least some portion of shells that are crushed by predators are too fragmented to be included in an analysis such as DUSDA.

Identical damage frequencies (no significant differences between drilled and undrilled groups) for a given damage category may have one of two causes: 1) the type of damage is only caused by taphonomic damage, so the frequencies are the same for each group, or 2) the type of damage is caused by both crushing predation and taphonomic forces, but it occurs so frequently as taphonomic damage that any predatory frequency is overwhelmed and undetectable. For this reason, the damage type with the largest Frag%$_P$, being the largest minimum frequency, is probably the most accurate proxy for the actual mortality due to crushing predation in the gastropod population. Thus, Frag%$_{Pmax}$ equals the Estimated Minimum Crushing Mortality (EMCM) for the species.

In addition to estimating the frequency of predatory damage, DUSDA also indicates which types of damage are more likely to be predatory, i.e., which types of damage were more frequent in undrilled shells. If a certain type of damage, e.g., apex damage, occurs with roughly equal frequency in drilled and undrilled shells, it can be considered primarily a type of taphonomic damage. If that type of damage occurs only in undrilled shells and never in drilled shells, it is characteristic of damage caused by a crushing predator. In cases where the damage occurs in the drilled shells but is much more frequent in undrilled shells, it can be inferred that that type of damage can be caused taphonomically, but can also be the result of predatory crushing.

### *2.5. Statistical Analysis*

For the purpose of displaying the results visually, the numbers of damaged and undamaged drilled and undrilled shells were expressed as percentages or decimal frequencies. For statistical analysis, however, the damage frequencies of drilled and undrilled shells were compared by using the raw counts of the group with the smaller sample size and standardizing the counts of other group to the smaller sample size. For example, there were 228 drilled and 197 undrilled *Nassarius perpinguis*. The raw numbers of damaged and undamaged drilled *N. perpinguis* were standardized so that they totaled 197. Standardizing to the smaller sample size allows one to compare the frequencies statistically and maintain a conservative result.

The standardized data were compared using the binomial test (Zar 1984) to see whether the damage frequencies were truly different or statistically indistinguishable. The Sequential Bonferroni correction (Rice 1989) was performed on the resulting p-values to account for multiple tests applied to the same data set.

### *2.6. Resampling*

For three of the study species (*Olivella biplicata, Nassarius perpinguis,* and *Euspira lewisii*), 100 specimens (50 drilled and 50 undrilled) were randomly selected and were re-examined for damage. The resulting damage frequencies were compared to those calculated in the initial examination to ensure that the results were replicable.

## 3. RESULTS

For each species, the frequencies of certain types of damage were found to differ significantly between the drilled and undrilled groups. The types, and number of types, differed from species to species. (See Table 2)

### *Olivella biplicata*

The drilling frequency for *O. biplicata* was 15% (146 drilled shells, 849 undrilled shells). Six out of the eleven potentially predatory damage types were significantly more common in undrilled shells after Sequential Bonferroni correction (see Table 2). The differences in frequencies between undrilled and drilled shells ranged from -0.2% to 16.4%; the greatest difference is the Estimated Minimum Crushing Mortality, EMCM = 16.4%.

### *Olivella beatica*

The drilling frequency for *O. beatica* was 42% (162 drilled shells, 228 undrilled shells). No potentially predatory damage types were significantly more common in undrilled shells after Sequential Bonferroni correction (see Table 2). The differences in frequencies between undrilled and drilled shells ranged from -0.6% to 6.0% (EMCM = 6.0%).

### *Nassarius perpinguis*

The drilling frequency for *N. perpinguis* was 54% (228 drilled shells, 197 undrilled shells). No potentially predatory damage types were significantly more common in undrilled shells after Sequential Bonferroni correction (see Table 2). The differences in frequencies between undrilled and drilled shells ranged from -5.1% to 7.2% (EMCM = 7.2%).

*Euspira lewisii*

The drilling frequency for *E. lewisii* was 32% (138 drilled shells, 294 undrilled shells). Five out of the eleven damage types were significantly more common in undrilled shells after Sequential Bonferroni correction (see Table 2). The differences in frequencies between undrilled and drilled shells ranged from -0.3% to 19.8% (EMCM = 19.8%).

Certain damage categories were consistently greater in undrilled in three of the four study species (see Table 2). Deep aperture chips, extensive peeling, and columella damage were significantly more common in undrilled shells for two species.

Within species, certain categories of damage were not (or extremely infrequently) observed in the drilled groups but were observed in the undrilled groups (see Table 2). For most of the species, extensive aperture peeling and major body whorl damage occurred only rarely in drilled specimens.

### *3.1. Resampling*

Resampling of 50 drilled and 50 undrilled individuals was performed for *Olivella biplicata*, *Nassarius perpinguis*, and *Euspira lewisii*. In almost all cases, the sign (positive or negative) of the difference between the damage frequencies of drilled and undrilled shells was the same in resampling as in the original sampling. For example, in the original sampling, aperture abrasion was more frequent in undrilled *O. biplicata* than in drilled specimens. In resampling, aperture abrasion was again more frequent in undrilled shells, indicating that the original results are replicable. There were only three instances where the sign of the difference reversed in resampling (Table 2). Only one of these cases involved a damage category that differed *significantly* between drilled and undrilled shells (*E. lewisii*: apex abrasion was significantly more common in undrilled shells in the original sampling, but was less common in undrilled shells in resampling).

## 4. DISCUSSION

Using Drilled-Undrilled Shell Damage Analysis, certain types of shell damage (deep aperture chips, extensive aperture peeling, and columella damage) were more frequent in undrilled shells than in drilled shells, indicating that crushing predation is to some degree responsible for damage. Additionally, certain types of damage (deep aperture chips, extensive aperture peeling, and major body whorl damage) occur rarely if at all in drilled specimens, suggesting that they are indeed indicative of crushing predation and not caused by taphonomic forces. P-values for aperture removal were significant for three of the four species before Sequential Bonferroni correction, suggesting that these may be borderline cases. These types of damage are the same types that have been observed in crab crushing experiments and attributed to crushing predation when observed in the fossil record (Vermeij et al. 1980, Bertness and Cunningham 1981, Allmon et al. 1990, West et al. 1991, Donovan et al. 1999). Importantly, the gastropod species in this study represented a broad range of morphologies, especially with respect to aspect ratio, ranging from long and narrow-apertured to globose and wide-apertured, further suggesting that the above damage types are predatory in origin and not due to random taphonomic forces. DUSDA also showed that certain types of damage are more likely to have taphonomic origins: aperture abrasion and shallow aperture chips tended to occur on both undrilled and drilled shells. In some cases, the damage frequencies were very similar but still exhibited a significant difference due to the large sample sizes involved. This suggests that those types of damage can be caused by predatory attacks or taphonomic forces.

A full interpretation of these results requires a closer examination of the factors, in addition to true crushing predation mortality, that may influence the calculated EMCMs. The study taxa are similar in that they are infaunal and lack projecting ornament such as large spines or varices. Their main active defense against durophagous predators such as decapod crustaceans (e.g., the spiny lobster, a major denizen of San Diego waters, and crabs in the genus *Cancer*) may be their ability to burrow into soft sediment to avoid or escape certain benthic predators. Infaunality likely does not protect them from drilling naticids (*Euspira lewisii* itself is the major drilling naticid in the area), which are themselves often infaunal. This difference may account for the high drilling frequencies and low estimated minimum crushing frequencies of *Olivella beatica* (drilling frequency 42%, Estimated Minimum Crushing Mortality 6.0%) and *Nassarius perpinguis* (drilling frequency 54%, EMCM 7.2%); the taxa are simply more vulnerable to drilling predation than to crushing predation. This line of reasoning, however, does not seem to apply to *O. biplicata* (drilling frequency 15%, EMCM 16.4%)

and *E. lewisii* (drilling frequency 32%, EMCM 19.8%), which both have lower drilling frequencies and higher EMCMs than *O. beatica* and *N. perpinguis*. One possible explanation for *E. lewisii* is that drilling rates are suppressed because cannibalism is inherently dangerous. An individual *E. lewisii* that attempts to drill a conspecific may be meeting its own predator; a non-naticid mollusk is a safer choice of meal. Note, however, that incomplete naticid predatory boreholes were common among non-bored *E. lewisii* (see Table 2).

The differences between the smaller, thinner-shelled gastropods and the larger, thicker-shelled gastropods may be due to differences in prey preference on the part of the predators. Drilling predators generally are much smaller than crushing predators and may prefer smaller (*O. beatica*) or thinner shelled (*N. perpinguis*) prey, while crushing predators may prefer larger, higher-yield prey (*O. biplicata* and the extremely meaty *E. lewisii*). Thus, higher drilling frequencies and lower crushing frequencies would be expected in *O. beatica* and *N. perpinguis*. Detailed research into the drilling and crushing predators in the environment would be required to ascertain whether this is indeed the case.

### *4.1. Non-predatory Causes of Damage to Gastropod Shells*

Differences in damage frequencies may also be due to non-predatory or taphonomic factors. Wave action is one potential source of taphonomic damage. Water can roll empty shells along the sediment-water interface or push shells against rocky surfaces, causing abrasion and other damage. However, experiments have shown that typical fair-weather wave action is probably not capable of causing the type of catastrophic damage associated with crushing predation. Jory & Iversen (1988) found that the forces required to crush shells of the tropical snail *Strombus gigas* (13.4 mm to 238.0 mm in length) ranged from 31 N to 24,908 N (the 238.0 mm shell failed to break at even >31,000 N). In experimental measurements of claw closing force in the North American Pacific Northwest (where intertidal gastropod sizes tend to range from ~5-50mm), the xanthid crab *Lophopanopoeus bellus* exerted a force of 25.5 N (Behrens Yamada and Boulding 1998). Boulding (1984) measured *Cancer productus* crushing forces up to 178 N. In another study, the average maximum bite force of *C. productus*, based on mechanical advantage, was calculated to be 132.1 N (Taylor 2000). The forces created by ocean waves, on the other hand, are typically much lower. For example, the measured forces on the limpet *Lottia pelta* on an exposed Washington, USA shore did not exceed 5N (Denny 1985).

Buried shells may be compacted and cracked by the overburdening sediment and tectonic stress (Zuschin et al. 2003). These are probably not major sources of damage to shells found on the sediment surface, but subsurface collections and certainly fossil collections can be subject to these forces.

Shells are also subject to shell weakening processes due to the environment or other organisms. Chemical dissolution by seawater or by acidic conditions produced by microorganisms changes the microstructure and mechanical properties of the shell, as well as creating a rough or weathered appearance (see Zuschin et al. 2003 and references therein). Boring organisms, such as certain barnacles, bryozoans, foraminifers, polychaetes, and clionid sponges, bore into the shells of living gastropods and shells inhabited by hermit crabs (see next paragraph) (Smyth 1990). Boring can result in visible holes and can also compromise the structural integrity of the shell, making it more vulnerable to taphonomic damage (Zuschin et al. 2003). While dissolution and boring, unlike other forms of non-predatory damage, are unlikely to be confused with predatory damage, the consequent weakening of the shell structure can make shells more susceptible to taphonomic damage.

A major source of post-mortem damage to gastropod shells is hermit crabs, which inhabit empty shells (Walker 1989). Over the course of a shell's existence, countless crabs may inhabit the shell, exposing it to ecological and environmental conditions that are not necessarily the same as those the gastropod experienced. Shells can incur damage from predation (intentional or mistaken) on the hermit crabs (possibly by the same predators that target gastropods); environmental (taphonomic) forces like wave action; and boring organisms such as sponges and spionid worms against which gastropods, but not hermit crabs, can defend (Walker 1989). Hermit crabs effectively extend the "lifetime" of the shell to many times the natural life of the original gastropod inhabitant. Laboratory experiments have found that hermit crabs prefer undamaged over damaged shells (Bulinski 2007) and intact shells over drilled shells (Pechenik and Lewis 2000) when given the choice.

Two types of non-predatory damage that may indicate hermit crab inhabitation were measured in the present study. Pinhole borings and extensive boring traces can be formed by boring organisms against which snails, but not hermit crabs, defend (Walker 1989). These categories were found to be significantly more frequent on drilled than undrilled shells, possibly indicating that undrilled shells had higher rates of hermit crab habitation. However, pinhole borings are not an absolute indication of hermit crab habitation. They may also be interpreted as muricid predatory boreholes. Muricid boreholes were not identified and included in the drilled shell groups; muricid boreholes should be more frequent in the undrilled groups (gastropods already killed by naticids will not be drilled by muricids). Pinhole drill rates were very low among the drilled groups, as would be expected. If muricid-drilled shells are among the undrilled shells, all damage frequency estimates are conservative. Extensive boring traces are more likely to point to hermit crab habitation. If extensive boring traces are assumed to be positive evidence of hermit crab habitation, the frequency of extensive boring trails in drilled shells represents a hermit-habitation baseline. One can calculate the difference in habitation rates between drilled and undrilled shells to estimate how much hermit crab habitation may bias the results of DUSDA. The additional habitation rates (beyond the habitation baseline calculated from drilled shells) for undrilled shells (calculated as Damage%U - Damage%D) ranged from 0.25% to 7.5%. Revised EMCMs can be calculated assuming that all of the additional inhabited undrilled shells were damaged. The resulting EMCMs (see Table 3) of three of the species are still positive, indicating that the damage measured in DUSDA cannot be fully explained by hermit crab habitation. Only *Olivella beatica*, which had the smallest original EMCM, has an additional habitation rate greater than its original EMCM.

In many environments, hermit crab populations can be very dense and empty shells are often a limited resource (Fotheringham 1976 and references therein, Bulinski 2007). The hermit crab population utilizes almost all shells, even those drilled and otherwise damaged, so all habitable shells are exposed to the same types and degrees of taphonomic damage. Even when hermit crabs are not using all types of shells to the same extent, it is possible to examine the shells for evidence of hermit crab habitation and to account for habitation in the analysis. As long as the degree of hermit crab habitation can be ascertained, the DUSDA method is valid.

### *4.2. Crushing Predation's Influence on Gastropod Shell Form*

The potential influence of predation on the evolution and ecology of organisms points to the need for techniques like Drilled-Undrilled Shell Damage Analysis that can be used to investigate the relationship between predation and gastropod characteristics. One of the major arguments supporting the importance of durophagous predators in the evolution of mollusks, gastropods in particular, is the observation that potentially anti-predatory shell features have increased (i.e., become more common and more extreme) throughout gastropod history (Vermeij 1977, Palmer 1979, Vermeij 1987). These traits include increased shell thickness, increased shell sculpture (ribs, spines, or varices), and narrow apertures. These features have all been suggested to be anti-predatory, by either deterring predators or interfering with grappling and handling, and some studies have demonstrated that ornament indeed can have an anti-predatory function (Palmer 1979, Stone

1998, Donovan et al. 1999). The appearance and diversification of these features may have coincided with, and have been interpreted as evidence for, the increase in predation intensity that marks the Mesozoic Marine Revolution (Walker and Brett 2002). Infaunality of molluscs, which was uncommon before the Mesozoic, has also been interpreted as being at least in part anti-predatory (Aberhan et al. 2006). There is evidence from modern systems that suggest features such as shell sculpture are anti-predatory. Bertness and Cunningham (1981) found that crabs are more successful at crushing gastropods with thin shells and wide apertures. Laboratory experiments have found that some gastropods build better-defended shells in the presence of chemical cues from crushing predators. *Nucella lamellosa* produced larger apertural teeth (Appleton and Palmer 1988) and a thicker shell (Bourdeau 2009) in the presence of the major gastropod crusher *Cancer productus*. Bourdeau (2009) did not find this response to a non-crushing predator (the seastar *Pisaster ochraceus*). Laboratory grown *Littorina obtusata* produced thicker shells in the presence of their major crushing predator, *Carcinus maenas* (Trussel 2000). In natural environments, gastropods in low-energy, high-predation environments have been found to have thicker shells than conspecifics in high-energy, low-predation environments (Boulding et al. 1999). Given the evidence, it is possible that gastropod shell features such as increased thickness and ornament (along with other physiological and behavioral traits) evolved in response to crushing predation.

### *4.3. Modeling Dead Shell Populations*

While the above features may have anti-predatory evolutionary origins, the presence or absence of these features may not permit concrete statements about the influence of predation on the evolution of various gastropod taxa. Data on possible defensive features must be correlated with more-direct evidence of predation, like predatory attack rates, attack success rates, and prey mortality, and with phylogenetic data to seal the link between the evolution of shell features and durophagous predation. DUSDA is one tool that may provide valuable data on prey mortality due to crushing predation both in modern environments and the fossil record. The caveats outlined above point to the fact that comparisons of drilling frequencies and EMCMs are more challenging among taxa that differ morphologically or ecologically. Several factors contribute to the final distribution of the shell population:

1. Real crushing mortality: the actual percentage of the total population that is killed by crushing predation. This is a direct measure for crushing predation intensity on the population. The crushing mortality is the product of the predatory attack rate and the attack success rate.

2. Frequency of crushed shells that are destroyed: a certain number of crushed prey will be obliterated by the predator. This is in turn influenced by the size, morphology, and shell characteristics (thickness, defensive ornament) of the prey (for example, *Nassarius perpinguis* has a much thinner shell than *Euspira lewisii* and thus may be more susceptible to total destruction) and by predator characteristics, namely prey preference and crushing ability (predators that are

able to completely destroy a given prey individual may actually ignore that individual and choose a larger individual that supplies greater nutrition but whose shell is resistant against complete destruction). Due to the nature of the destroyed shell material, quantification of this variable is probably impossible in the fossil record and extremely difficult in the modern.

3. Real drilling frequency: the actual percentage of the total population that is killed by drilling predation. Drilled shells may be more susceptible to taphonomic damage than undrilled shells, and thus drilling frequencies are underestimated. However, the number of undrilled shells that have been destroyed by crushing predation may be much higher. The total shell population is thus reduced, so calculated drilling frequencies may be higher than the real drilling frequency. Unfortunately, it is not easy to determine the degree to which drilling frequencies are overestimated (see variable 2, above). While the drilling frequency does not directly factor into the calculation of the EMCM, it could conceivably influence the true crushing predation mortality of a prey population: drilled individuals are removed from the potential prey population for crushing predators, capping the potential crushing mortality at a lower rate than if drilling predation were not a factor. However, because crushing predators are larger and more powerful than drilling predators, and because crushing predators often prey on the drillers themselves (for example, crushing predation on the driller *Euspira lewisii*), drilling predation will not likely overwhelm and limit crushing predation. Drilling predation rates should be taken into account when considering EMCM in

the context of *total mortality* of the prey population (by predatory and non-predatory causes).

4. Frequencies of taphonomic removal: all shells have a chance of being destroyed by post-mortem factors (biotic and abiotic). However, not all shells are equally susceptible. As mentioned in variable 3, drilled shells may be more vulnerable to taphonomic damage than intact shells because the borehole has weakened the shell. The ante- and perimortem history of the shell influences its susceptibility to post-mortem damage. Intact, drilled, and crushed (excluding those shells destroyed by crushing) shells probably have different frequencies of taphonomic removal, intact shells being the least susceptible and crushed shells being the most susceptible. Thus, the EMCM is again an underestimate, because crushed shells are more likely to have been lost taphonomically than drilled or intact shells. The assumption that the frequencies of taphonomic removal are equal among all shells results in a highly conservative estimate of crushing predation.

The above four factors are quantifiable. They are added into an equation that describes the composition of a dead shell population:

$$(\text{Total Population} = N) = (\text{Drilled Shells} = D) + (\text{Crushed Shells} = C) + (\text{Intact Shells} = I)$$

where Intact Shells are those that died of causes other than drilling or crushing predation. For the purposes of the model, it is assumed that these other causes of death do not cause shell damage.

The frequency of the whole population that bear complete predatory boreholes is $\%_D$, the drilling frequency. The total number of drilled shells is

$$D = N * \%_D.$$

Drilled shells can be further divided into shells that are present ($D_P$) in the assemblage and shells that have been removed by taphonomic means ($D_R$):

$$D_R = D * (\text{drilled removal frequency} = \%_{RD})$$

$$D = (D * \%_{RD}) + D_P$$

The number of crushed shells depends on the attack frequency ($\%_A$) and the attack success frequency ($\%_S$). The frequency of shells killed by crushing ($\%_C$) is the product of the previous two frequencies:

$$C = N * (\%_A * \%_S) = N * \%_C$$

Some crushed shells are completely destroyed during the event. These totally crushed shells ($C_T$) are lost to the record:

$$C_T = (N * \%_C) * \%_T$$

The crushed shells, like drilled shells, can be divided into present ($C_P$) and taphonomically removed shells. The removed shells ($C_R$) are described thus:

$$C_R = C * (\text{crushed removal frequency} = \%_{RC})$$

$$C = (C * \%_{RC}) + C_P$$

The remaining shells that are not drilled or crushed are considered Intact. Intact shells can be divided into taphonomically removed shells ($I_R$) and present shells ($I_P$). Intact present shells are divided into hermit crab-inhabited shells ($I_{PH}$) and non-inhabited shells ($I_{PO}$).

$$I = N - D - C$$

$$I_R = I * (\text{intact removal frequency} = \%_{RI})$$

$$I = (I * \%_{RI}) + I_P$$

$$I_{PH} = (I – [I * \%_{RI}]) * (\%_H = \text{hermit habitation rate})$$

$$I = I_R + I_{PH} + I_{PO}$$

In this model, hermit crabs are assumed to inhabit only pristine (intact) shells, never drilled or crushed shells. In reality, hermit crabs often inhabit sub-optimal shells.

Because of the various removal variables, the dead shell assemblage observed in modern environments or the fossil record is not the same as the original dead shell population. In a dead shell assemblage, what remains are the present drilled shells ($D_P$) and the present undrilled shells. The undrilled shells (U) can be described as:

$$U = C_P + I_P = C_P + I_{PH} + I_{PO}$$

$$U = (C - C*\%_{RC}) + ([I - I*\%_{RI}]* \%_H) + (I - I*\%_{RI})$$

The variables that are missing from the dead shell assemblage ($D_R$, $C_T$, $C_R$, and $I_R$) have the potential to impact the interpretation of the DUSDA results.

Using a hypothetical population of 10,000 dead shells, the frequency variables (drilling frequency and crushing frequency, removal frequencies of crushed and intact shells; hermit crab habitation frequency of present intact shells, original damage frequency of crushed shells, and damage frequency of hermit crab-inhabited shells) were isolated and adjusted to see their effect on the predicted EMCM (the damage frequency of undrilled shells in the dead shell assemblage). The original damage frequency of crushed shells can represent any of the damage categories outlined in this paper (or any other conceivable type of shell damage caused by crushing predation). Because the removal frequency of drilled shells does not factor into the calculation of the damage frequency of undrilled shells, it will not have an effect on the EMCM.

Baseline values of model variables: Because only one variable is manipulated at a time, values were assigned to the variables to set a baseline against which the results of manipulations of the model are compared. For each run of the model, all variables are baseline except the variable that is being tested:

Drilling frequency = 0.30
Crushing frequency = 0.60
Intact frequency = 1.0 – (0.30 + 0.60) = 0.10
Removal frequency drilled = 0.05
Removal frequency of crushed shells: 0.05
Removal frequency intact: 0.05
Hermit habitation frequency of intact shells: 0.50
Original damage frequency of crushed shells: 0.20
Damage frequency of hermit inhabited shells: 0.20

The baseline values were chosen in an attempt to approximate potential real-life values of the model variables. The drilling frequency is a moderate estimate based on the observed drilling frequencies in the study assemblages (ranging 0.147 to 0.536). The crushing frequency estimate is speculative; actual crushing frequencies likely vary greatly between taxa and environments. The frequency of intact shells is calculated using the drilling and crushing frequencies. This assumes that drilling and crushing predation are the major causes of death in the shell population; that is, causes of death that leave the shell completely intact do not limit the gastropods available for drillers and crushers. The removal frequencies of drilled, crushed, and intact shells are set equal to assume that taphonomic conditions are the same for all groups of shells. The hermit crab habitation frequency assumes that shells are abundant enough that intact shells are available to all hermits; if shell availability were lower, hermit crabs would begin to inhabit drilled and crushed shells, but any consequent increases in taphonomic damage to these shells would be accounted for in calculation of the taphonomic baseline. The original damage frequency of crushed shells is set equal to the damage frequency of hermit inhabited shells, assuming that durophagous predation on hermit crabs equals that on the living gastropods themselves.

All of the above variables were manipulated individually in the model to see how variation in each variable can affect the resulting EMCM. The first result of the model, using the baseline values, is an EMCM of 0.1857, which is a conservative estimate compared to the “known” original damage frequency of crushed shells (0.20).

When drilling frequency is increased (Figure 9a), with crushing frequency held at 0.60, the EMCM approaches 0.20. This is because any effect from intact shells (hermit crab inhabited and non-inhabited) is removed when the number of intact shells goes to zero (the denominator of the EMCM, undrilled shells, become equal to the crushed present shells). In reality, hermit crabs would switch to drilled and crushed shells; any additional damage would be accounted for in the calculation of the taphonomic baseline. When drilling frequency is decreased, the EMCM decreases as the influence of intact shells becomes stronger: the number of intact, non-hermit inhabited shells increases, thus increasing the denominator (total undrilled shells) of the EMCM. At a drilling frequency of 0.01, the EMCM is reduced to 0.1606.

When the crushing frequency is increased (Figure 9b), with drilling frequency held at 0.30, the EMCM approaches 0.20, again because the effect of intact shells is eliminated. When crushing frequency decreases, the intact shells (both hermit inhabited and non-inhabited) cause the EMCM to decrease.

Increasing the removal frequency of crushed shells (Figure 9c) lowers the EMCM, again because the relative contribution of intact shells to the EMCM increases. At a removal frequency of 0.5 (half of all crushed shells are removed taphonomically), the EMCM is 0.1759. In turn, decreasing the removal frequency increases the EMCM: a removal frequency of zero results in an EMCM of 0.1863, which is still a conservative estimate of the original damage frequency of crushed shells. Overall, the impact of crushed shell removal frequency is minor: in reality, the removal frequency of crushed shells is not likely so high, while the removal frequencies of drilled and intact shells remain extremely low. Predictably, increasing the removal frequency of intact shells (Figure 9d) has an inverse effect: as the frequency approaches zero, the EMCM approaches 0.20. Again, this is because the influence of intact shells is removed from the calculation of the EMCM.

When the removal frequencies of crushed and intact shells are adjusted, but kept equal, their relative influence on the EMCM stays the same and the EMCM does not change.

Increasing the habitation frequency of hermit crabs (Figure 9e) in intact shells, the EMCM approaches 0.20, because the damage frequencies of crushed shells and hermit inhabited shells are set equal. When the damage frequency of hermit-inhabited shells is increased (Figure 9f), with the habitation frequency set at the baseline of 0.50, the EMCM can increase to values greater than the original damage frequency of crushed shells. A hermit-inhabited damage frequency of 1.0 results in an EMCM of 0.2429. However, the hermit-inhabited damage frequency is unlikely to be so much higher than the original damage frequency of the crushed shells. Such a difference would imply that crushing predators preferred hermit crabs and that predation on live gastropods was mistaken. When the damage frequency of inhabited shells is more reasonable (0.50), but still higher than the damage frequency of crushed shells, the EMCM is 0.2071, which is still greater than the original damage frequency of crushed shells, but much closer. The hermit-inhabited damage frequency is the only variable that has the potential to overestimate the EMCM relative to the original damage frequency of crushed shells. At the baseline values of the model, the EMCM is 93% the value of the original damage frequency. When the original damage frequency and the hermit-inhabited damage frequencies are changed, but kept equal to one another, the proportional difference between the original damage frequency and the EMCM is constant. When the original damage frequency is much greater than the hermit-inhabited damage frequency, the proportional difference increases: when the original damage frequency is 0.50 and the hermit-inhabited damage frequency is 0.20, the EMCM is 0.4429, which is 89% of 0.50.

Finally, the model was manipulated to reflect actual data from this study. Possible original drilling frequencies and crushing frequencies were back-calculated for *Olivella biplicata* by setting the number of drilled specimens (147) and the number of undrilled specimens (849) to their actual values in the dead shell assemblage. Baseline removal frequencies of 0.05 were retained for drilled shells and intact shells. The removal frequency of crushed shells was increased to 0.15 to account not only for shells lost taphonomically, but also for shells that were completely destroyed by crushing predation. Hermit crab habitation frequency was kept at 0.50, as in the model. With the crushed shell damage frequency and the hermit-inhabited damage frequency both set at 0.20, the calculated EMCM is 0.1695, approximate to the study EMCM of 0.164. The necessary drilling and crushing frequencies to create this result were 0.1370 and 0.6199, respectively, out of a total original population of 1,120 shells.

To test whether crushed shells in the original population would have been significantly more damaged than drilled shells, the original numbers of drilled and crushed shells bearing damage were determined: 153 drilled shells, 694 crushed shells (the number of crushed shells is less than the number of undrilled shells because not all undrilled shells were necessarily victims of predation). To determine the number of damaged and undamaged shells in each group, the taphonomic damage frequency (calculated from drilled shells in the original

DUSDA for *O. biplicata*) is added to the damage frequencies used in the model. The taphonomic damage frequency of deep aperture chips, 0.158, was used because this is the damage frequency from which the EMCM was drawn. The resultant damage frequencies are 0.158 for drilled shells and 0.358 (0.20 + 0.158) for crushed shells. Application of these frequencies results in 24 damaged drilled shells and 248 damaged crushed shells.

Finally, the numbers of damaged and undamaged drilled and crushed shells were standardized and compared using the binomial test (see Methods for a description). The resulting p-value was much less than 0.0001, a highly significant result. Thus, using the baseline variables of the model, it is predicted that the original shell population would have significantly different rates of damage between drilled and crushed shell groups, with the difference representing the frequency of that damage caused by crushing predation.

The model was applied in the same way to the other three study species. For *Olivella beatica* and *Nassarius perpinguis,* it was assumed that the calculated EMCM did represent mortality due to predation, despite the fact that no potentially predatory damage were significant for these two species. For *Euspira lewisii*, as with *O. biplicata*, the model yielded highly significant results ($p \ll 0.0001$). For *O. beatica*, the model yielded significant results ($p = 0.0059$), while the model did not yield significant results for *N. perpinguis* ($p = 0.9998$). The contrast between highly significant model results (*O. biplicata* and *E. lewisii*) and less- or non-significant model results (*O. beatica* and *N. perpinguis*) agrees with the general result that *O. biplicata* and *E. lewisii* had many significant damage categories, while *O. beatica* and *N. perpinguis* had none.

When interpreting the results of any study, the data and the study system must be examined for possible sources of bias. In the case of DUSDA, the question is in what direction, and to what degree, would the bias under- or overestimate the EMCM. For the most part, the potential biases in the dead shell assemblage result in EMCMs that slightly underestimate the original damage frequency of crushed shells; thus, EMCMs are generally conservative. The hermit-inhabited damage frequency, when greater than the original damage frequency, can inflate the EMCM. This does assume, however, that hermit crabs only inhabit pristine, “intact” shells. In reality, hermit crabs are generally limited in their choice of shells and must utilize crushed and drilled shells. Any additional damage incurred on these shells because of hermit inhabitation should be accounted for in the calculation of the taphonomic baseline. Examination of the shells for signs of hermit crab habitation can also clarify the influence of hermit crabs on the shell population.

## 5. CONCLUSIONS

Drilled-Undrilled Shell Damage Analysis will be a useful tool in examining crushing predation mortality in modern and ancient environments. DUSDA uses drilled shells to create baseline taphonomic damage frequencies, eliminating the need to distinguish between predatory and taphonomic damage on a per-individual basis; the method can account for types of predatory damage beyond what is easily recognizable. Unlike shell repair scar frequency, DUSDA is based on damage from successful attacks rather than unsuccessful attacks, so the results truly represent predatory mortality in the prey population. DUSDA can be applied to any dead shell assemblage that contains a sufficient number of drilled shells, so it has applications in modern environments and the fossil record.

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**Table 1**. Summary of sample sizes and drilling frequencies for the four study species.

| | Total | Drilled | Undrilled | Frequency |
|---|---|---|---|---|
| *Olivella biplicata* | 995 | 146 | 849 | 0.147 |
| *Olivella beatica* | 390 | 162 | 228 | 0.415 |
| *Nassarius perpinguis* | 425 | 228 | 197 | 0.536 |
| *Euspira lewisii* | 363 | 138 | 225 | 0.380 |

**Table 2**. Summary of counts and frequencies of damage categories for the study species. Asterisks indicate p-values significant at alpha=0.05 after Sequential Bonferroni Correction. Double asterisks indicate where the sign of the difference between drilled and undrilled shells reversed in resampling (see 3.1. Resampling).

| **Taxon** | | apex abrasion | apex removal | aperture abrasion | shallow chip | deep chip | extensiv peeling | body whorl damage | crack-aperture | crack-body whorl | hole-body whorl | columel damage | pinhole boring | extensiv boring | incomp drill |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Olivella* | Drilled (N=146) | **61** | **9** | **137** | **89** | **23** | **0** | **0** | **3** | **2** | **3** | **1** | **6** | **8** | **3** |
| *biplicata* | *Frequency* | *0.418* | *0.062* | *0.938* | *0.610* | *0.158* | *0.000* | *0.000* | *0.021* | *0.014* | *0.021* | *0.007* | *0.041* | *0.055* | *0.021* |
| | Undrilled | **418** | **95** | **840** | **643** | **273** | **59** | **26** | **16** | **11** | **76** | **73** | **317** | **136** | **18** |
| | *Frequency* | *0.492* | *0.112* | *0.989* | *0.757* | *0.322* | *0.069* | *0.031* | *0.019* | *0.013* | *0.090* | *0.086* | *0.373* | *0.160* | *0.021* |
| | *difference* | 0.075 | 0.050 | 0.051 | 0.148 | 0.164 | 0.069 | 0.031 | -0.002 | -0.001 | 0.069 | 0.079 | 0.332 | 0.105 | 0.001 |
| | p-value | 0.0426 | 0.0293 | 0.0000* | 0.0001* | 0.0000* | 0.0000* | 0.0107 | 0.7036 | 0.7066 | 0.0007* | 0.0000* | 0.0000* | 0.0001* | 0.6246 |
| | significant? | no | no | yes | yes | yes | yes | no | no | no | yes | yes | yes | yes | no |
| *Olivella* | Drilled (N=162) | **38** | **23** | **136** | **43** | **6** | **1** | **0** | **4** | **13** | **0** | **1** | **3** | **22** | **0** |
| *beatica* | *Frequency* | *0.235* | *0.142* | *0.840* | *0.265* | *0.037* | *0.006* | *0.000* | *0.025* | *0.080* | *0.000* | *0.006* | *0.019* | *0.136* | *0.000* |
| | Undrilled | **45** | **45** | **205** | **67** | **13** | **7** | **3** | **9** | **17** | **0** | **2** | **37** | **48** | **0** |
| | *Frequency* | *0.197* | *0.197* | *0.899* | *0.294* | *0.057* | *0.031* | *0.013* | *0.039* | *0.075* | *0.000* | *0.009* | *0.162* | *0.211* | *0.000* |
| | *difference* | -0.037 | 0.055 | 0.060 | 0.028 | 0.020 | 0.025 | 0.013 | 0.015 | -0.006 | 0.000 | 0.003 | 0.144 | 0.0750 | 0.000 |
| | p-value | 0.0497 | 0.0407 | 0.0119 | 0.2411 | 0.1778 | 0.0394 | 0.1172 | 0.2295 | 0.6770 | 1.0000 | 0.5843 | 0.0000* | 0.0100 | 1.0000 |
| | significant? | no | no | no | no | no | no | no | no | no | no | no | yes | no | no |
| *Nassarius* | Drilled (N=228) | **125** | **24** | **194** | **67** | **34** | **10** | **3** | **0** | **0** | **0** | **7** | **47** | **3** | **1** |
| *perpinguis* | *Frequency* | *0.548* | *0.105* | *0.851* | *0.294* | *0.149* | *0.044* | *0.013* | *0.000* | *0.000* | *0.000* | *0.031* | *0.206* | *0.013* | *0.004* |
| | Undrilled | **98** | **31** | **173** | **72** | **39** | **13** | **1** | **0** | **0** | **0** | **11** | **67** | **11** | **1** |
| | *Frequency* | *0.497* | *0.157* | *0.878* | *0.365* | *0.198* | *0.066* | *0.005* | *0.000* | *0.000* | *0.000* | *0.056* | *0.340* | *0.056* | *0.005* |
| | *difference* | -0.051 | 0.052 | 0.027 | 0.072 | 0.049 | 0.022** | -0.008 | 0.000 | 0.000 | 0.000 | 0.025 | 0.134 | 0.0430 | 0.001 |
| | p-value | 0.9328 | 0.0136 | 0.1173 | 0.0149 | 0.0411 | 0.0921 | 0.9202 | 1.0000 | 1.0000 | 1.0000 | 0.0728 | 0.0000* | 0.0010* | 0.3669 |
| | significant? | no | no | no | no | no | no | no | no | no | no | no | yes | yes | no |
| *Euspira* | Drilled (N=138) | **50** | | **138** | **106** | **38** | **13** | **2** | **5** | **9** | **0** | **27** | **9** | **5** | **2** |
| *lewisii* | *Frequency* | *0.362* | *0.000* | *1.000* | *0.768* | *0.275* | *0.094* | *0.014* | *0.036* | *0.065* | *0.000* | *0.196* | *0.065* | *0.036* | *0.014* |
| | Undrilled | **149** | | **294** | **241** | **119** | **63** | **27** | **23** | **21** | **0** | **116** | **101** | **18** | **35** |
| | *Frequency* | *0.505* | *0.015* | *0.997* | *0.817* | *0.403* | *0.214* | *0.092* | *0.078* | *0.071* | *0.000* | *0.393* | *0.342* | *0.061* | *0.119* |
| | *difference* | 0.143** | | -0.003 | 0.049 | 0.128 | 0.119 | 0.077 | 0.042 | 0.006 | 0.000 | 0.198 | 0.277 | 0.0250 | 0.104 |
| | p-value | 0.0005 | 0.4307 | 1.0000 | 0.0875 | 0.0012 | 0.0002 | 0.0002 | 0.0376 | 0.4768 | 1.0000 | 0.0000* | 0.0000* | 0.1474 | 0.0000* |
| | significant? | yes | no | no | no | yes | yes | yes | no | no | no | yes | yes | no | yes |

**Table 3**. Comparison of original Estimated Minimum Crushing Frequencies (EMCM) with recalculated EMCMs ($EMCM_H$). $EMCM_H$ is calculated by subtracting the estimated additional hermit crab habitation frequency of undrilled shells (Dam%U – Dam%D) from the original EMCM. All $EMCM_H$s but one are positive, indicating that for these three species, the damage cannot be completely explained by hermit crab habitation.

| | Total | Drill % | EMCM | $EMCM_H$ |
|---|---|---|---|---|
| *Olivella biplicata* | 995 | 0.147 | 16.4% | 5.9% |
| *Olivella beatica* | 390 | 0.41538 | 6.0% | -1.5% |
| *Nassarius perpinguis* | 425 | 0.53647 | 7.2% | 2.9% |
| *Euspira lewisii* | 363 | 0.38017 | 19.8% | 17.3% |

**Figure 1**. The potential relationships between the repair frequency of a gastropod population and predator attack frequency (predatory attempts per total prey population), attack success frequency (kills per total attacks; this may increase with increasing predator ability or may decrease with increasing prey defensive ability), and predation pressure (the prey mortality due to predation). Note that both an increase and a decrease in predation pressure can result in increases in repair frequency.

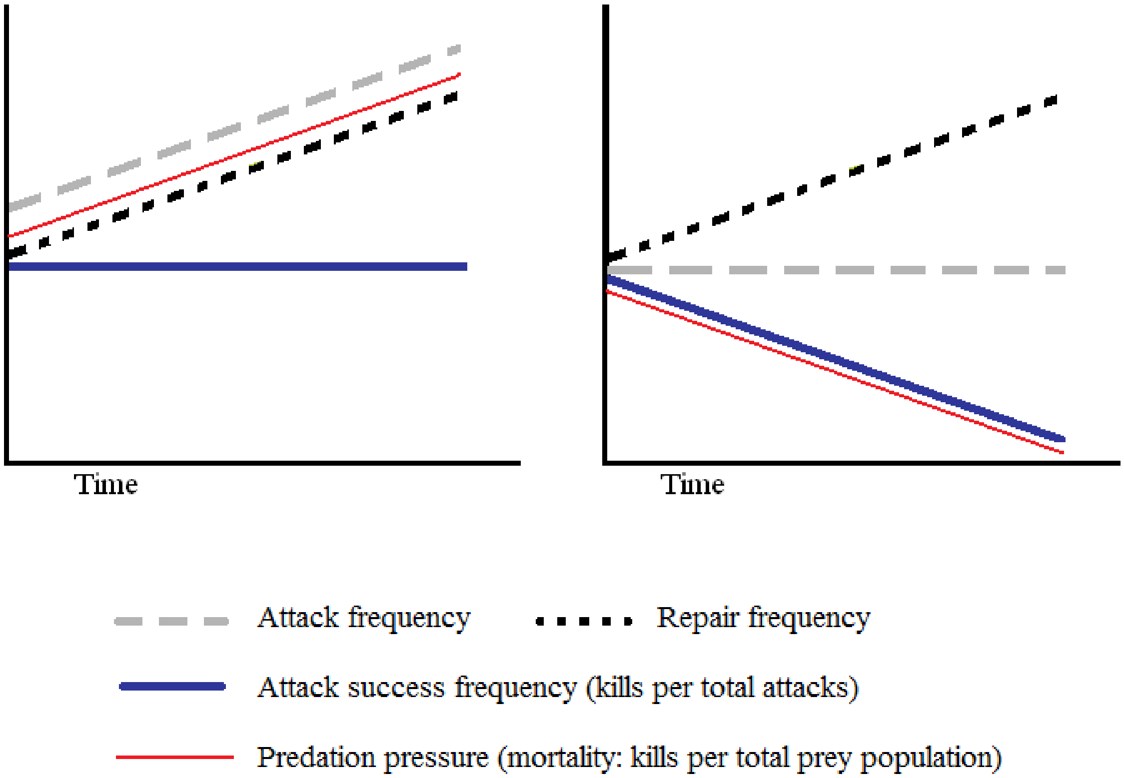


**Figure 2.** Both drilled and crushed shells can experience the same taphonomic forces. Line A shows the original predatory damage to the shell. In Line B, the same types of taphonomic damage have been added to both shells.

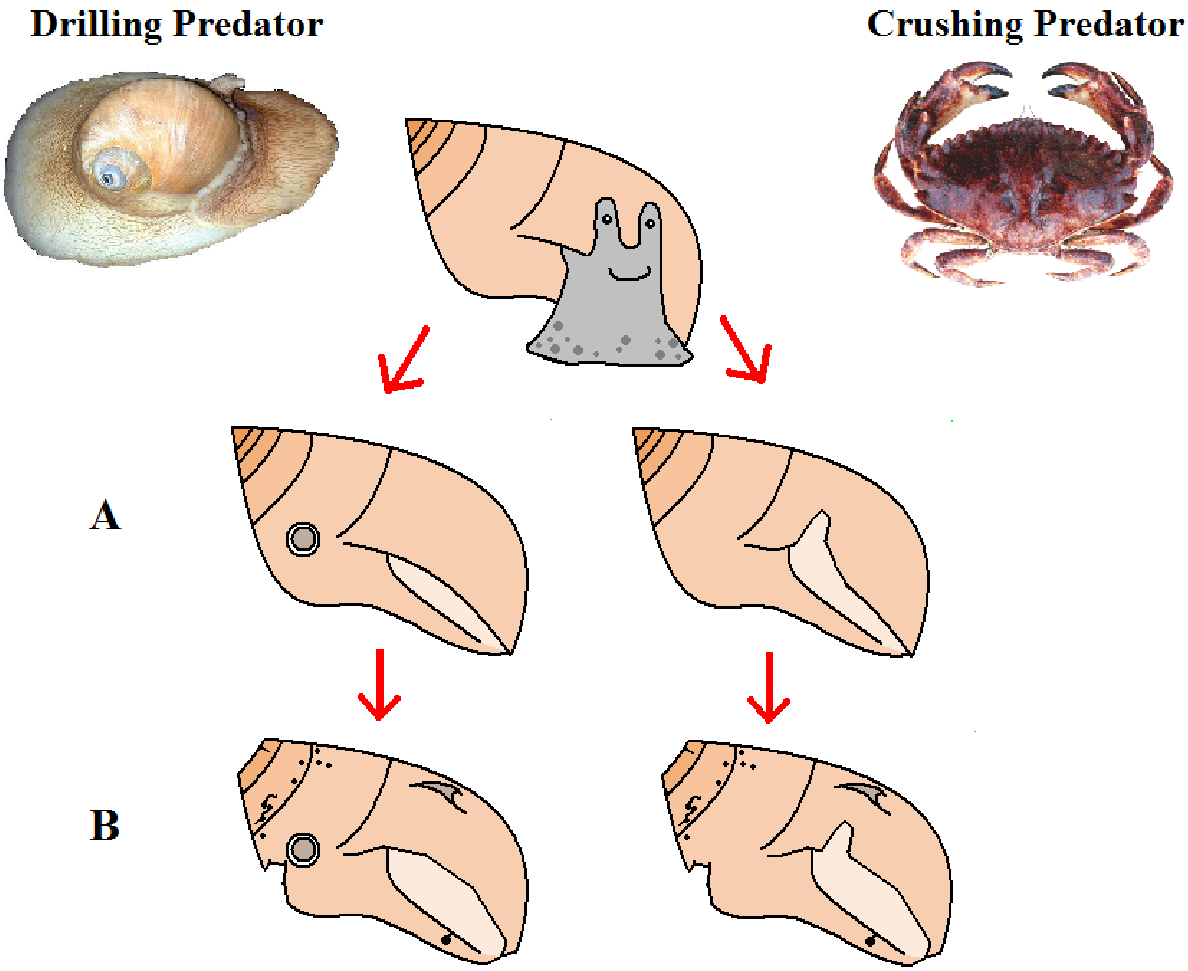


**Figure 3**. These hypothetical damage frequencies for drilled and undrilled shells demonstrate how the Estimated Minimum Crushing Mortality (EMCM) is calculated as the mathematical difference between the undrilled and drilled damage frequencies. For each damage category (A-E), the estimated damage frequency due to crushing predation is represented by the distance between the tops of the drilled and undrilled bars; the actual value is given below each set of bars. The greatest of these values, in this case 0.30, is the EMCM for the dead shell assemblage.

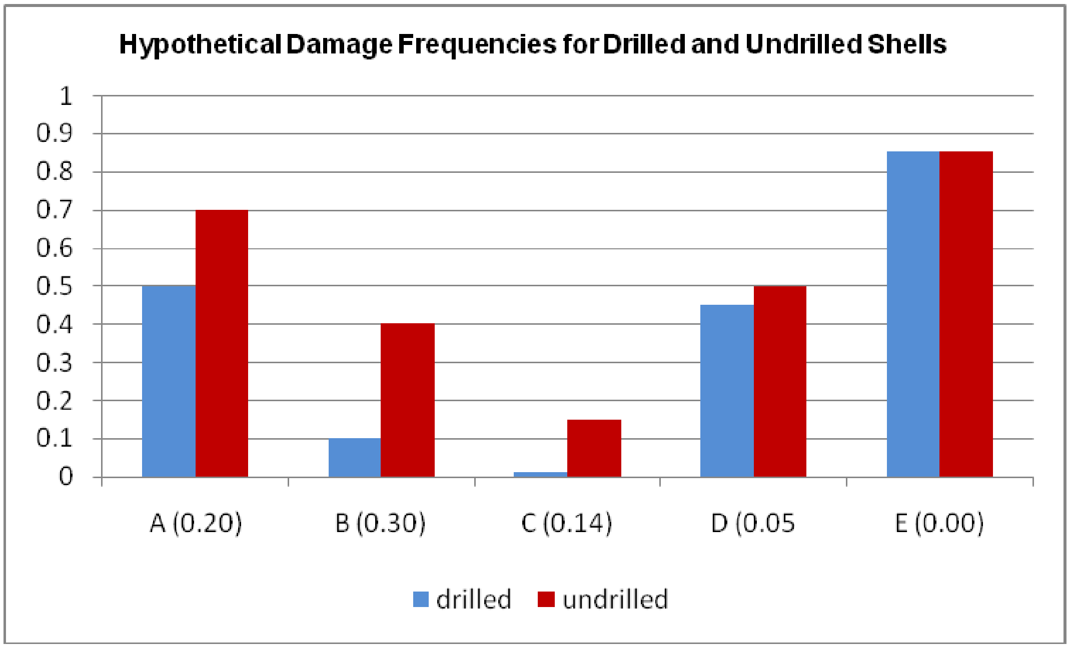


**Figure 4**. Illustration of a characteristic peel performed by a crab on a gastropod. The left drawing represents an intact shell. The right drawing represents a shell that has been peeled by a crab, leaving a wedge-shaped cutout in the aperture.

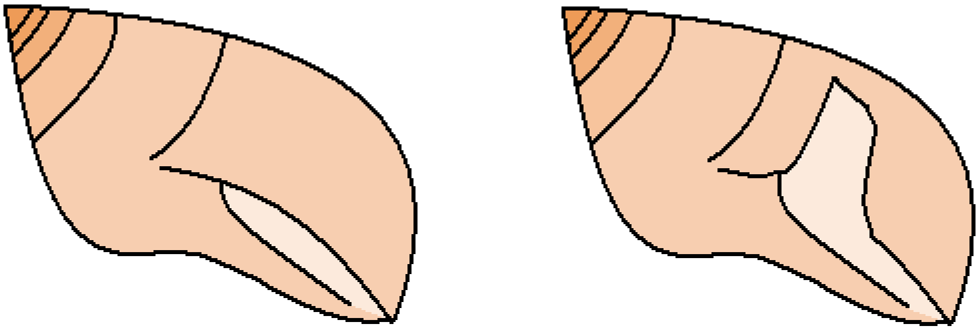


**Figure 5.** Photograph of a typical naticid predatory drill hole. Note the beveled rim of the hole, a product of the hole's conical cross section. The victim of this drilling is a naticid itself, *Euspira lewisii*, one of the four species in this study and the taxon that probably produced these holes. Scale is in centimeters.

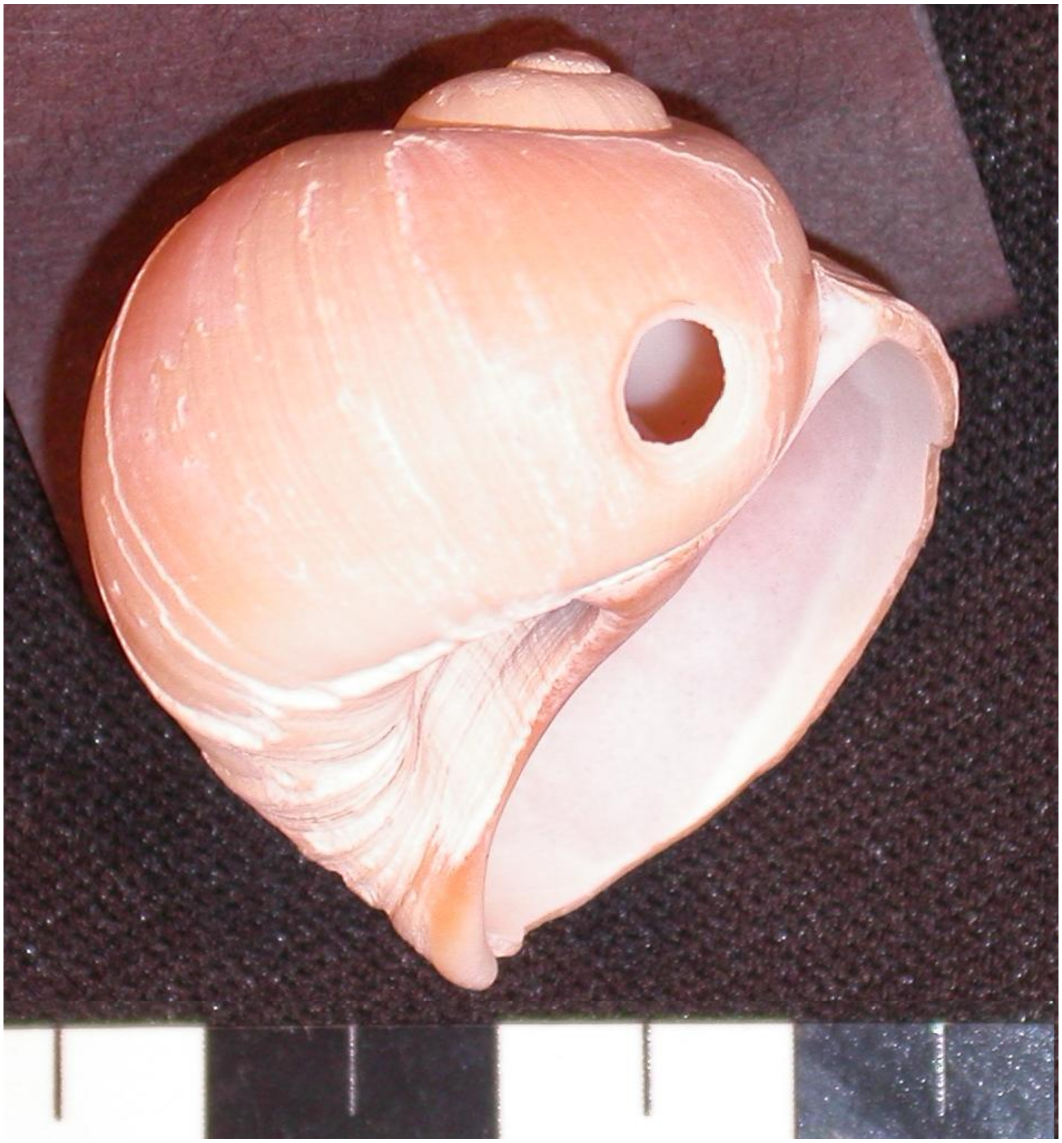


**Figure 6.** Example photographs of the four species used in this study: a. *Olivella biplicata*, b. *Olivella beatica*, c. *Nassarius perpinguis*, d. *Euspira lewisii*. The *O. biplicata* in this figure has a naticid predatory drill hole. Note the landmark penultimate whorl (the whorl immediately above the body whorl) on *O. biplicata, O. beatica,* and *N. perpinguis*. On *E. lewisii*, note the plastered region where the suture meets the wide apertural margin (the landmark for this species). Scales are in centimeters.

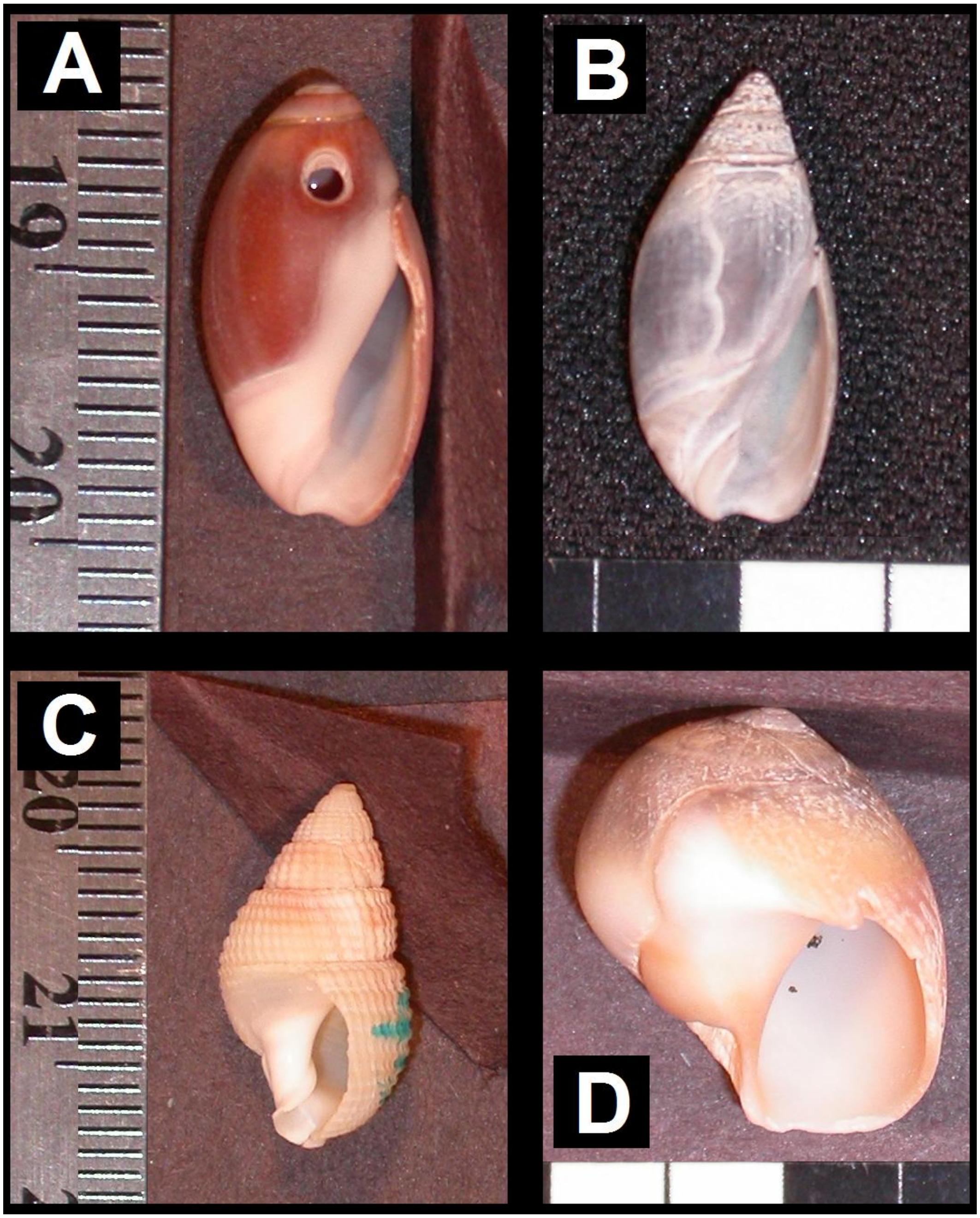


**Figure 7.** Photographs of *Olivella biplicata* illustrating the various damage categories tallied on the four study species. A. Apex removal; B. Apex abrasion and aperture abrasion; C. Shallow aperture chip (and naticid predatory drill hole); D. Deep aperture chip; E. extensive aperture peel; and F. Major body whorl damage and columella damage. All scale bars are 1 cm.

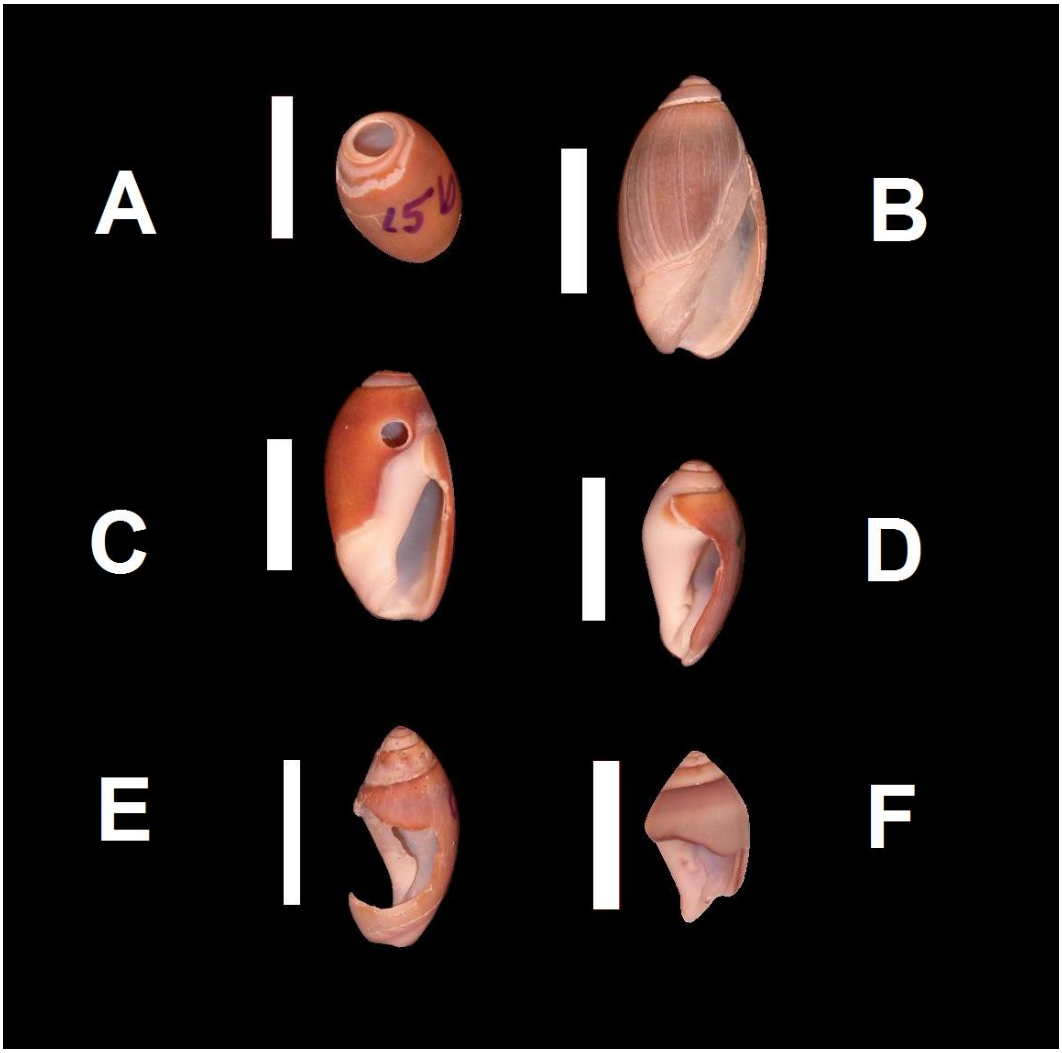
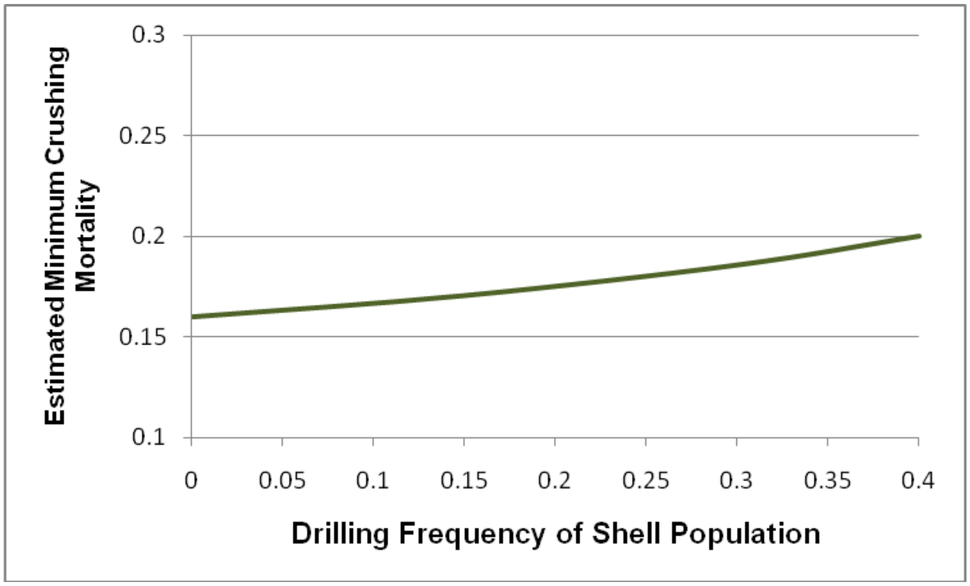


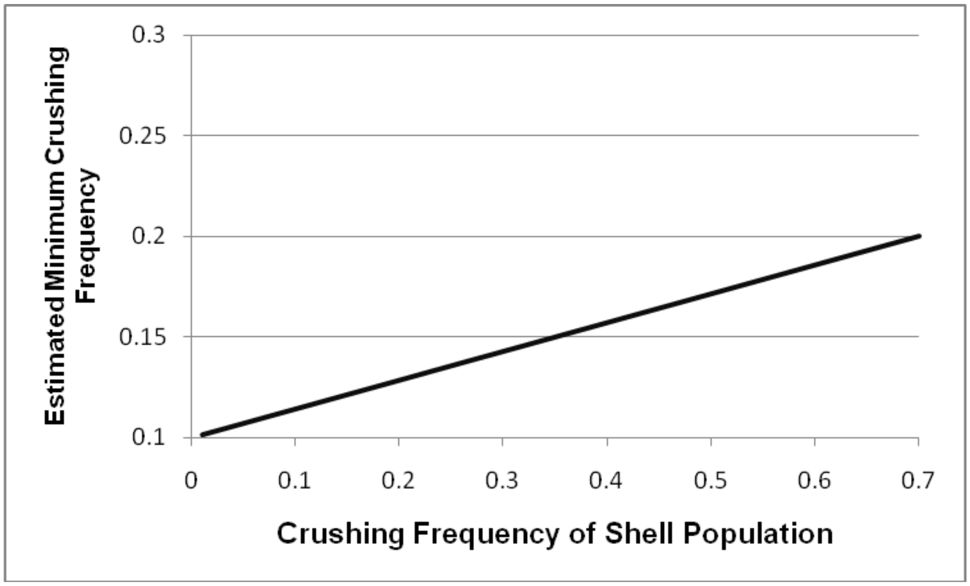
**Figure 8.** Photograph of *Olivella biplicata* illustrating extensive boring traces, a form of non-predatory shell damage. Scale bar is 1 cm.

**Figure 9**. Graphs illustrating the effects of various variables on the calculated Estimated Minimum Crushing Frequency, where the “known” original damage frequency of crushed shells is 0.20.

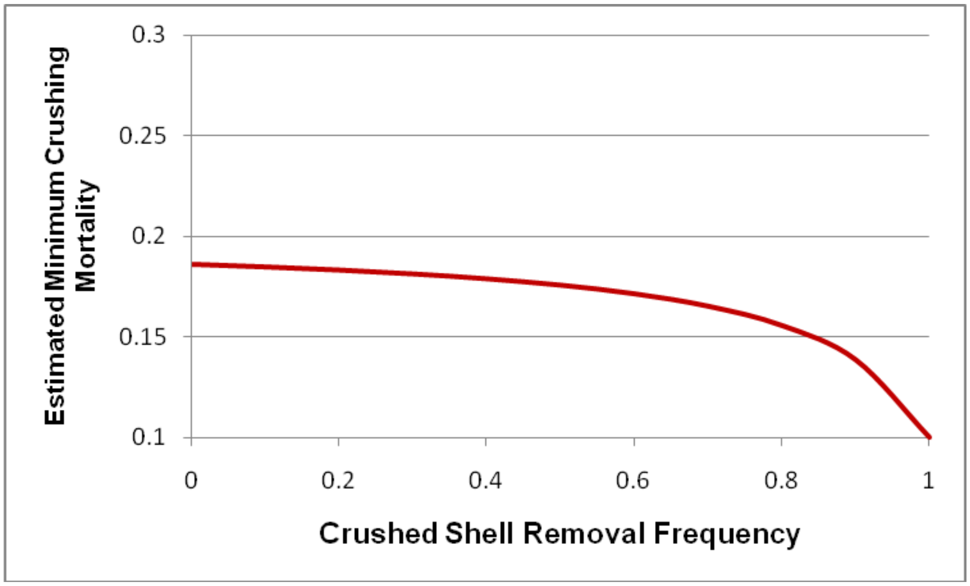
a.



b.

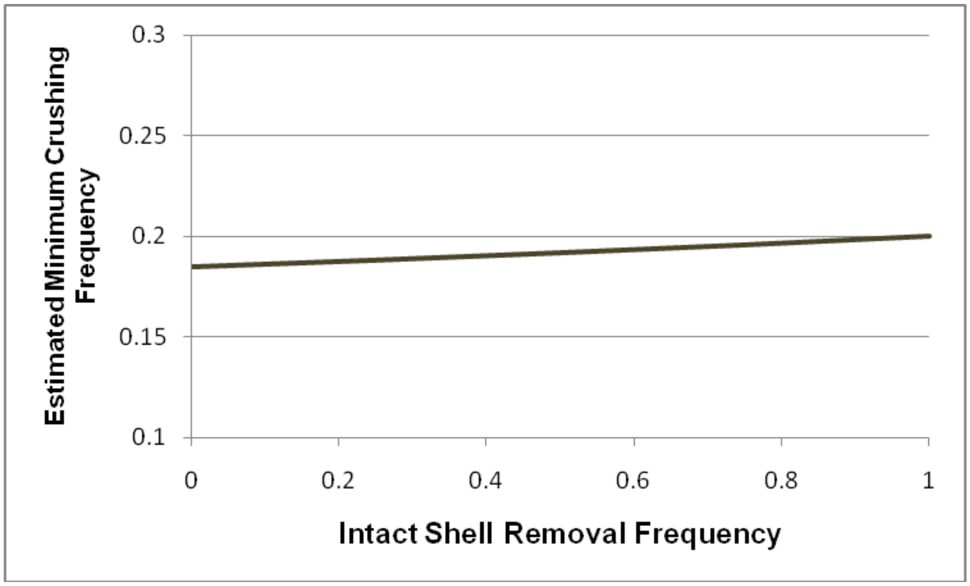


c.



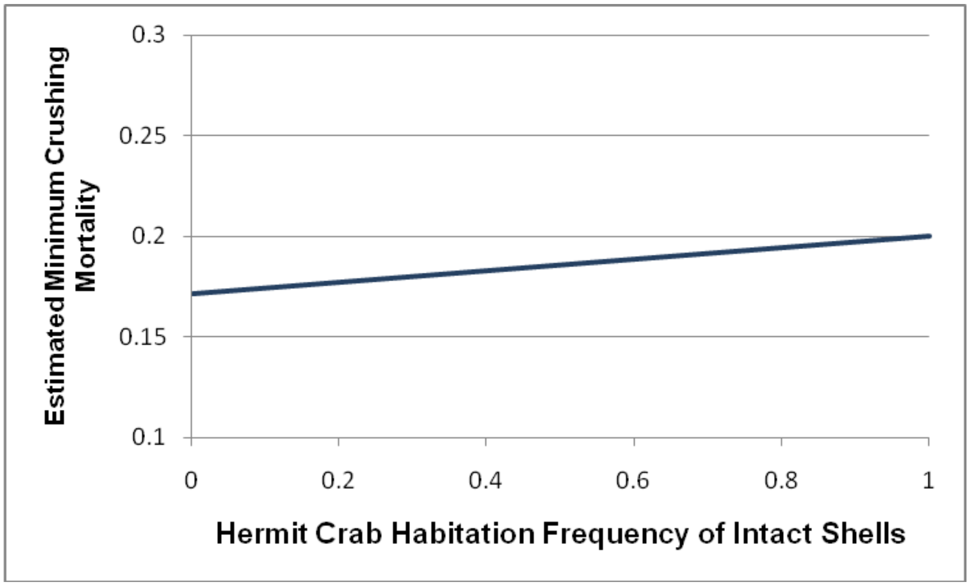
Estimated Minimum Crushing Mortality
0.3
0.25
0.2
0.15
0.1
0
0.2
0.4
0.6
0.8
1
Crushed Shell Removal Frequency

d.

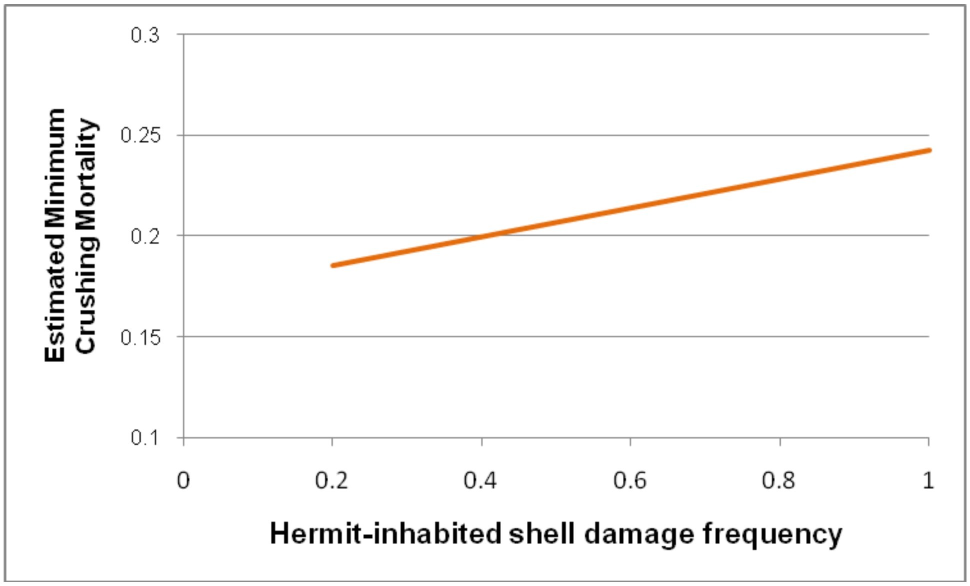


Estimated Minimum Crushing Frequency
0.3
0.25
0.2
0.15
0.1
0
0.2
0.4
0.6
0.8
1
Intact Shell Removal Frequency

e.


Estimated Minimum Crushing Mortality
0.3
0.25
0.2
0.15
0.1
0
0.2
0.4
0.6
0.8
1
Hermit Crab Habitation Frequency of Intact Shells

f.


Estimated Minimum Crushing Mortality
0.3
0.25
0.2
0.15
0.1
0
0.2
0.4
0.6
0.8
1
Hermit-inhabited shell damage frequency