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Pictured is a trench on the eastern side of the quarry (east of Sarasota, FL) in which samples were collected. Sampling location (along the lowest wall) in SMR Aggregates Quarries Phase 10 (north is toward the foreground of the image).

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Spatial Variation in Predation in the Plio-Pleistocene Pinecrest Beds, Florida, USA

Frank L. Forcino^{1*}, Holly J. Hurding-Jones, and Emily S. Stafford¹

Abstract - We examined six temporally equivalent assemblages distributed across 700 m in the Plio-Pleistocene Pinecrest beds (Tamiama Formation, southern Florida) and found significant spatial variability in predation trace frequencies (drillholes and repair scars) among marine mollusks (ranging from 0.03 to 0.11 for all mollusks combined). We then explored potential causes for the variability we observed. Overall, there was little inter-sample variability in diversity metrics (generic richness, evenness, and Shannon-Wiener Index) and paleocommunity composition or characteristics (i.e., life modes and feeding strategies). The variation in predation trace frequencies suggests that a single sample from a locality may be insufficient to represent the predation patterns of the entire bed.

Introduction

One of the major goals in studying predation among marine macroinvertebrates in the fossil record is to discern how predation has shaped evolution and ecosystems through time (see Alexander and Dietl 2003, Vermeij 1987). In order to interpret temporal patterns, it is important that potential within-bed spatial variability in predation is also identified and taken into account (e.g., Hansen and Kelley 1995, Hoffmeister and Kowalewski 2001, Huntley and Scarponi 2015). In this study, we examined six temporally equivalent fossil assemblages from the Plio-Pleistocene Pinecrest beds of the Tamiama Formation in southern Florida. We quantified spatial variability in predation trace frequencies and taxonomic makeup, then explored potential causes for the variability we observed. Our goal was to determine whether a single sample would sufficiently represent the predation patterns and community makeup of the entire bed.

It is extremely rare to directly observe predation in the fossil record; typically, predatory interactions are identified indirectly, in the form of traces that record attacks (both successful and unsuccessful) on the prey's remains (Alexander and Dietl 2003, Leighton 2002, Vermeij 1987). Two common, relatively easy to identify predation traces on shelled marine invertebrates (e.g., mollusks and brachiopods) are drillholes and repair scars. Drillholes are formed by boring predators, which drill through the prey shell to kill and extract the animal within (Carriker 1961). Naticid and muricid gastropods are notable drillers; other potential drillers on mollusk prey or hosts include buccinid, capulid, marginellid, and nassariid gastropods and octopods (Kowalewski 2002). A complete drillhole (one that fully penetrates the prey shell) generally indicates a lethal attack (Carriker 1961, 1969; but see also Visaggi et al. 2013). Repair scars on the other hand, are the result of non-lethal attack on shelled prey by a durophagous predator (one that breaks the shell to access the prey, such as many crustaceans) (Alexander 1981, Alexander and Dietl 2003). A repair scar, distinguishable as deflection or deformation in shell growth lines or ornament, is typically interpreted as an indication that the prey survived the attack and regrew its shell (Vermeij 1987).

Predation can be affected by factors on many spatial scales, from meter-scale habitat variation to global latitudinal gradients. These factors can include substrate sediment content, nutrient availability, life mode, and biogeographic constraints (Bardhan et al. 2014,

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Sawyer and Zuschin 2010, Seitz et al. 2001, Vermeij 1987, Visaggi and Kelley 2015). At regional scales, Visaggi and Kelley (2015) hypothesized that the effects of temperature and seasonality on metabolic rates may explain the latitudinal drilling predation gradient in Brazil. Bardhan et al. (2014) linked low predation on mollusks to the biogeographic restriction of drilling predators from the study region. At more local scales, Sawyer and Zuschin (2010) noted spatial variation in drilling predation among different nearshore marine environments. Seitz et al. (2001) found that habitat and life mode affect crushing predation; focusing on predation frequencies and mortality between sandy and muddy habitats. Their subsequent model showed that infaunal prey were less likely to be preyed upon. Chattopadhyay et al. (2015) found a similar result for drilling predation; but see Leonard-Pingel and Jackson 2013 for a contrasting result. Kitchell et al. (1981) found naticid predators to be prey selective depending on the size and type of prey, as have many others (e.g., Kelley 1988, Hansen and Kelley 1995); this suggests that spatial variation in both predator and prey distributions could also drive variation in predation.

Hoffmeister and Kowalewski (2001) found considerable spatial variation in predation at multiple spatial scales (as well as between taxonomic levels). Hansen and Kelley (1995) assessed spatial variation in drilling predation over bathymetric gradients, finding significant variation among samples, but no bathymetric patterns (finding that assemblage-level drilling frequencies correlated with diversity and with the relative abundance of preferred prey taxa). Cadée et al. (1997) found considerable variation in repair scar frequencies of modern gastropods among microhabitats within Bahía la Cholla, in the Gulf of California (Mexico). In the present study, we assess variation in drilling and repair frequencies over a relatively small transect (700 m north to south). If predation in the Pinecrest beds does vary spatially, this would suggest that single samples are insufficient for characterizing predation intensities, even over a small area, especially when considered in broader ecological or temporal contexts.

Geologic Setting

The Pinecrest beds occur in the uppermost Tamiami Formation, in southwestern Florida (Fig. 1), and were likely deposited during the late Pliocene and early Pleistocene (3–2 Ma, Missimer 2001). Through the early to late Miocene, the fauna from the Caribbean Gatunian province migrated northward into the Caloosahatchian province, including paleo-Florida (Vermeij 2005). Because of this migration, the bulk of molluscan taxa in the Pinecrest beds are tropical or subtropical (Ward 1992). During the mid-Pliocene warm period, global sea levels were 10–20 m higher, and temperature 2–3 °C warmer (Raymo et al. 1996, Williams et al. 2008). Upon the commencement of late Neogene glaciation, sea temperature and level dropped (Petuch 1982a, Stanley 1986). The exact conditions during the deposition of the Pinecrest beds are difficult to discern, as the Tamiami Formation was deposited during both the waning warm periods of the late Pliocene, and during times of glaciation (Williams et al. 2008). Extinctions persisted through the late Pliocene and Pleistocene to ca. 1–2 million years ago, lowering biodiversity through the end of, and after, the Tamiami Formation (Petuch 1995, Stanley 1986).

The Pinecrest beds were deposited on the west coast of paleo-Florida, and show gradual changes among beach, subtidal, intertidal, and lagoon environments (Missimer 1992, Petuch 1982b). Unit 7, the interval sampled for this study, represents a marginal marine environment, consists largely of gray quartz sand, and is highly fossiliferous (Missimer 1992, Petuch 1982b; Fig. 2A). The material is generally poorly lithified and easy to sample (Fig. 2B). The shell deposits of Unit 7 are dominated by well-preserved bivalves, gastropods, corals, and a smaller presence of fishes, crustaceans, and other marine organisms (Petuch 1982a, b).

Materials and Methods

We bulk-collected six one-gallon bag-sized sediment and fossil samples from Unit 7 of the Pinecrest beds, in Phase #10 of the SMR Aggregates Quarries, Sarasota County, Florida, in December of 2014 (Figs. 1, 2). The samples were spaced approximately 100–200 m apart (a total distance of 700 m between Samples 1 and 6) (Fig. 1).

After collection, the samples were washed to remove excess sand, then sieved to sort fossils into size classes. Specimens larger than 3 mm were used in this study. The 3 mm threshold was chosen for ease of identification of taxa and predation traces, but it should be noted that the choice of sieve mesh size can affect the paleocommunity, predation, and taphonomic patterns observed in an assemblage (Kowalewski and Hoffmeister 2003). The specimens were identified to genus level and counted. In cases where the genus could not be determined, the family was identified. When the family could not be identified, the specimen was not included in the analysis. Bivalves were counted using the minimum number of individuals method (MNI) used by Gilinsky and Bennington (1994), taking the

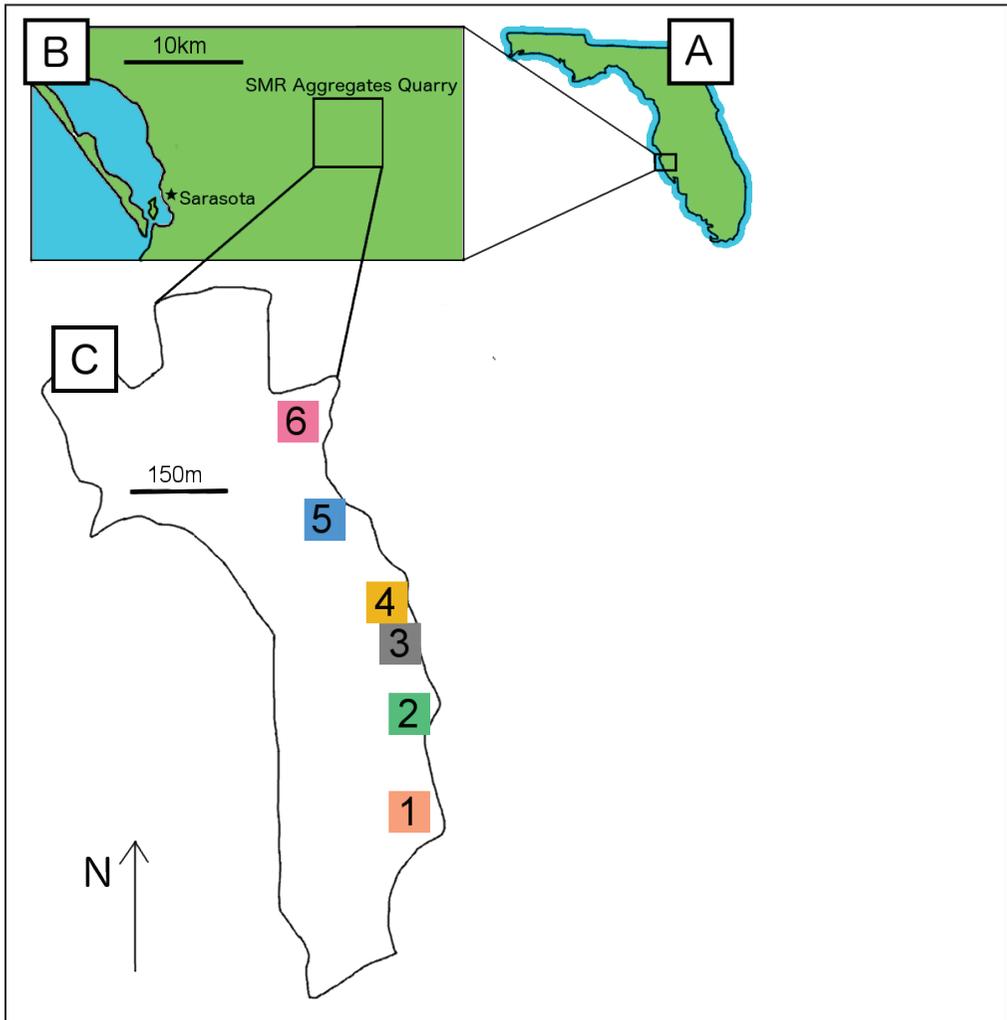


Figure 1. Location of SMR Aggregates Quarries Phase 10 (A) within Florida and (B) relative to Sarasota. (C) Locations of Samples 1 (peach), 2 (green), 3 (gray), 4 (yellow), 5 (blue) and 6 (pink) within the quarry.

highest respective number between left and right valves (using the umbo as a landmark to avoid double counting), to quantify total individuals present of each genus. Gastropods were counted using the shell spire as a landmark to avoid double counting. Miscellaneous fossils, such as corals, shark teeth, and urchin spines, as well as the tube-forming gastropod *Petalococonchus* Lea, were counted by how many individual pieces were present. Life mode and feeding habit were determined for bivalves, and feeding habit for gastropods, using the Molluscan Life Habits Database (Todd 2001).

Relative abundances, generic richness, Pielou's evenness, and Shannon-Wiener Index were calculated for each sample. The relative distributions of bivalve life modes, bivalve feeding strategies, and gastropod feeding strategies were determined. Sediment grain size analysis was performed to detect major variations in the physical environment.

Predatory repair scars and drillholes (Fig. 2, C and D) were counted on bivalves and gastropods. Specimens were counted as drilled if they had a complete, intact drillhole. Incomplete drillholes (those that do not fully penetrate the shell) and/or multiple drillholes on a single specimen were not observed in the assemblage. A specimen was counted as repaired if any amount of scarring was present on the shell, regardless of the size or number of scars. Drillhole frequency (DHF) and repair scar frequency (RF) were calculated as the number of individuals bearing the trace divided by the total abundance. In this calculation, the total abundance included some shells that were too fragmented to assess for predation traces; however, most of the counted shells were complete enough to determine whether drillholes or scars were present or absent, so total abundance was used. Although the resulting frequencies could be considered underestimates (if fragmented individuals bore traces that were not counted), excluding these specimens would likely overestimate frequencies (since specimens likely not bearing traces would be left out of the calculation). Because frequencies were generally low, including fragmented specimens yields more accurate frequencies.

Additional factors have the potential to bias predation frequencies in a sample, such as drillholes altering the taphonomic vulnerability of a shell (Roy et al. 1994; but see also Kelley 2008) or driving differential transport of valves (Chattopadhyay et al. 2013, Lever et al. 1961; but see also Molinaro et al. 2013). Either may result in drilling frequencies that are overestimated or underestimated, depending on the specific taxa and conditions.

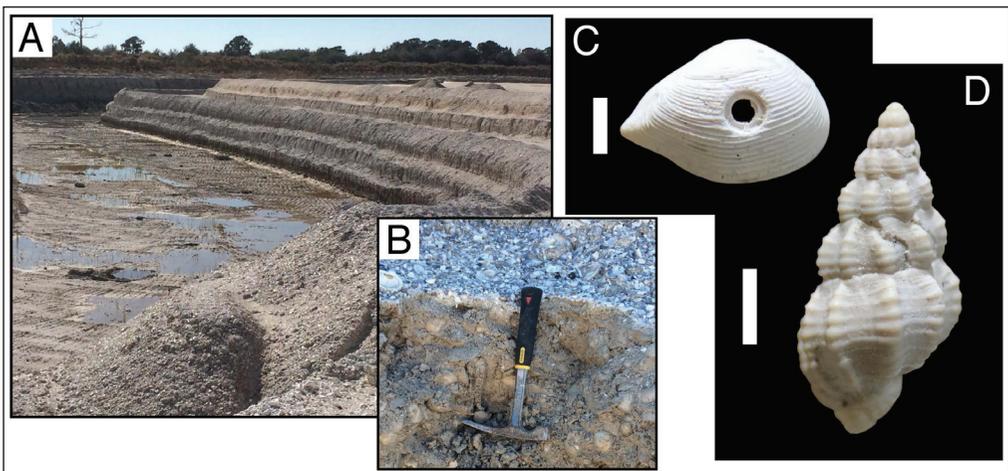


Figure 2. A. Pictured is a trench on the eastern side of the quarry in which samples were collected. Sampling location (along the lowest wall) in SMR Aggregates Quarries Phase 10 (north is toward the foreground of the image). B. Weakly lithified, highly fossiliferous sandstone. C. Predatory (naticid) drillhole on a corbulid bivalve. D. Crushing repair scar on second whorl of *Nassarius* Duméril.

Similarly, although the MNI method was used for counting bivalves, the total number of drilled or scarred specimens, regardless of whether a specimen was included in the MNI, was used to calculate frequencies. Tallying predation traces on all valves assumes that each trace-bearing valve represents a unique individual in the sample, and that there was no left/right valve preference by predators. Left/right valve drilling preferences tend to be expressed on prey that expose one valve in life position (Anderson 1992, Hasegawa and Sato 2009); whereas most prey usually exhibit no valve preference (Kelley 1982, Kingsley-Smith et al. 2003). For consistency, we tallied all predation traces the same way for all taxa.

Trace frequencies were calculated at the genus level, at higher taxonomic levels (bivalves, gastropods, and all mollusks), and for infaunal and epifaunal bivalves. Trace frequencies were also calculated for selected abundant genera to explore potential drivers of predation patterns. “Abundant” genera had an abundance of at least 15 individuals in at least one sample, or an abundance of at least 100 individuals totaled across all six samples.

Fisher’s exact tests (where $\alpha = 0.05$), corrected for multiple post-hoc pairwise comparisons, were used to statistically evaluate if trace frequencies differed spatially for the various taxonomic categories (Legendre and Legendre 1998, Mangiafico 2016). We employed corrected Fisher’s exact tests to test for significant differences between proportions of drilled to undrilled shells among all six samples. To test for any significant relationships between predation frequencies and ecological measures, life mode, feeding habits, or grain size, we conducted a series of spearman rank correlations (see Appendix A for tables of all spearman rank correlation results [see Supplemental File 1, available online at <https://eaglehill.us/epalonline/suppl-files/epal-004-forcino-s1.pdf>]).

Results

Paleocommunity metrics

Total number of specimens across all six samples was $n = 3055$. The assemblages were dominated by bivalves $n = 2285$ (75% among all samples), followed by gastropods $n = 740$ (24%), then all other organisms $n = 31$ (1%). Median sample size was $n = 509$, with a mean of $n = 509.2$. The lowest sample size was $n = 405$ for Sample 1 (southernmost site), and the largest was Sample 5 $n = 662$ (second-to-most northern sample). Common taxa included *Nuculana* Link (11% of all mollusk specimens), *Lucinisca* Dall (8%), and the combined genera of corbulid bivalves (13%). (See Appendix B for full dataset [see Supplemental File 2, available online at <https://eaglehill.us/epalonline/suppl-files/epal-004-forcino-s2.pdf>])

Richness varied from 51–67 genera, evenness ranged 0.72–0.84, and Shannon-Wiener Index ranged 2.83–3.40 (Fig. 3; See Appendix B for all diversity metrics). Relative abundances of bivalves to gastropods ranged from 84.0% bivalves, 16.0% gastropods (Sample 5) to 61.6% bivalves, 38.4% gastropods (Sample 6) (Fig. 4). Infaunal, free-living bivalves dominated the bivalve assemblages (overall 82.3%, Fig. 5). Suspension feeders dominated both the bivalve assemblages (average 63.7%, Fig. 6) and the gastropod assemblages (overall 66.3%, Fig. 7). (See Appendix B for full dataset)

Grain size analysis

Sediment was predominantly fine to coarse sand (> 0.125 mm; $> 90\%$ of grains), with coarse sand (> 1.00 mm) making up about 40% of total grains (Fig. 8). Distribution of grain sizes was consistent among the samples, with only a slight increase in the proportion of coarse sand in Sample 2.

Predation metrics

For mollusks overall, drillhole frequency (DHF) ranged from 0.025 (Sample 3) to 0.114 (Sample 2), with an overall frequency (all samples combined) of 0.076 (Fig. 9A). For gastropods, DHF ranged 0.006–0.134, with an overall frequency of 0.055 (Fig. 10A). For bivalves, DHF ranged 0.033–0.126, with an overall frequency of 0.083 (Fig. 10C). For infaunal bivalves, DHF ranged 0.031–0.139, with an overall frequency of 0.088 (Fig. 11A). For epifaunal bivalves, DHF ranged 2.4%–8.4%, with an overall frequency of 0.059 (Fig.

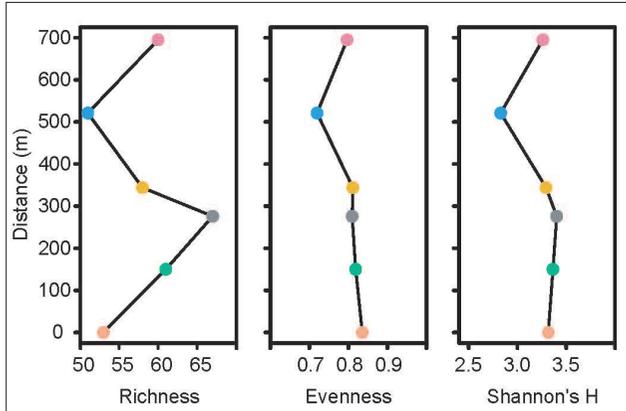


Figure 3. Generic richness, evenness, and Shannon-Wiener Index (Shannon's H) by sample. Samples from bottom (south) to top (north): 1 (peach), 2 (green), 3 (gray), 4 (yellow), 5 (blue) and 6 (pink).

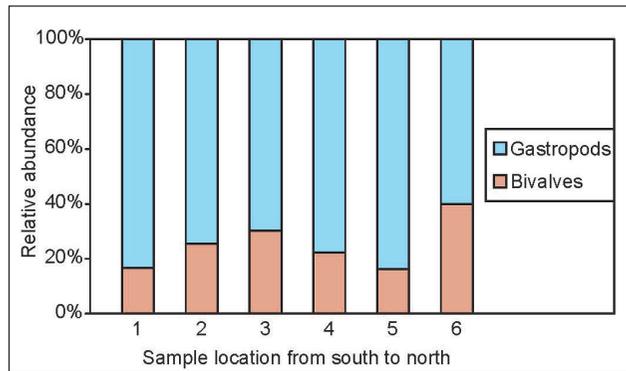


Figure 4. Relative abundance of bivalves and gastropods by sample.

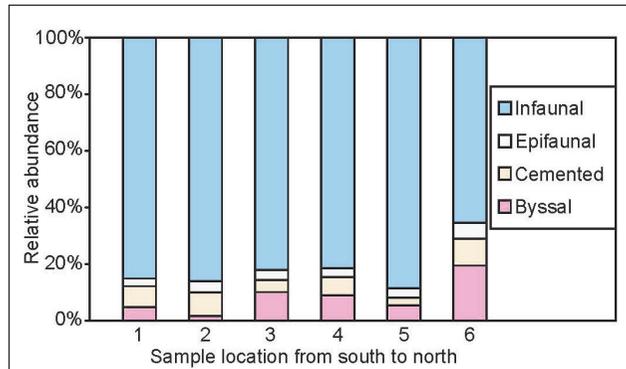


Figure 5. Relative abundance of bivalve life modes by sample.

11C) (See Appendix B for all predation metrics).

Mollusk repair frequency (RF) ranged 0.032 (Sample 3) to 0.134 (Sample 1), with an overall frequency of 0.055. (Fig. 9B). Gastropod RF ranged 0.006–0.107, with an overall frequency of 0.054 (Fig. 10B). Bivalve RF ranged 0.031–0.143, with an overall frequency of 0.056 (Fig. 10D). Infaunal bivalve RF ranged 0.033–0.154, with an overall frequency of 0.060 (Fig. 11B). Epifaunal bivalve RF ranged 0–0.085, with an overall frequency of 0.031 (Fig. 11D).

Overall trace frequencies (all samples combined) were also calculated for 20 “abundant” genera (those with an abundance of at least 15 individuals in at least one sample, or with at least 100 individuals summed over all six samples), and were compared to the overall trace frequencies of the respective higher taxon (bivalves or gastropods). For all the abundant genera combined of bivalves combined, overall DHF = 0.088 (versus 0.083 for all bivalves) and overall RF = 0.061 (versus 0.056). For the abundant gastropod genera, overall DF = 0.035 (versus 0.055 for all gastropods) and overall RF = 0.057 (versus 0.054). Of the 20 genera, seven had DHF's higher than the higher-taxon frequency (and 13 were lower). For RF, 9 genera were higher than the higher-taxon frequency, and 11 were lower.

Three bivalve genera are of particular interest: *Lucinisca* had a very high overall abundance (246) and had an overall DHF = 0.199, but the similarly abundant *Nuculana* (n = 344) had a DHF of only 0.044. *Anodontia* Link (n = 40) had the highest overall DF (0.200) and the highest overall RF (0.575) among “abundant” genera.

Statistical analysis

In the statistical comparisons of DHF between samples (Table 1; corrected Fisher’s exact test, $\alpha = 0.05$), Sample 3 stood out with the most significant differences: For mollusks, Sample 3 differed from all five other samples; it differed from four other samples for both bivalves and gastropods. For mollusks, seven out of 15 comparisons were significant (five of 15 for bivalves, four of 15 for gastropods).

For RF comparisons (Table 1; corrected Fisher’s exact test, $\alpha = 0.05$), Sample 1 differed significantly from all five other samples for both mollusks and bivalves, and the only other significant difference was between Samples 2 and 3 (mollusks). For gastropods, Sample 3 differed from four other samples, and Sample 1 was different from only Sample 3.

Out of 90 total statistical comparisons of predation trace frequencies between samples, over one-third (33) were significantly different, more than expected due to chance (at $\alpha = 0.05$).

Overall, there were very few significant spearman rank correlations between predation trace frequencies and paleocommunity metrics, taxon relative abundances, life modes, feeding strategies, or grain size distribution (Appendix A). Two isolated exceptions were bivalve RF with evenness ($p = 0.003$) and gastropod RF with the relative abundance of byssal bivalves ($p = 0.03$).

The major exception to the overall lack of significant correlations is between predatory gastropod relative abundance and five predation frequencies: DHF

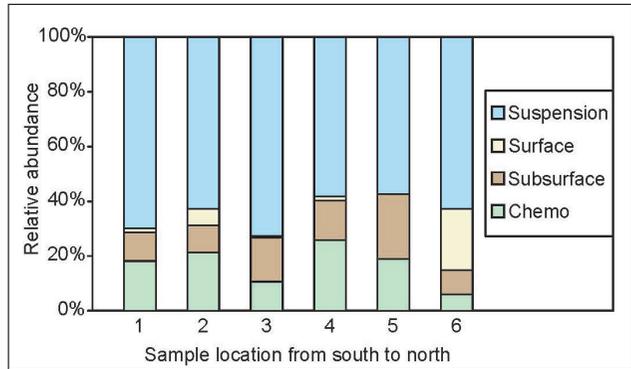


Figure 6. Relative abundance of bivalve feeding habits by sample. Suspension = suspension feeder; Surface = surface deposit feeder; Subsurface = subsurface deposit feeder; Chemo = chemosymbiotic

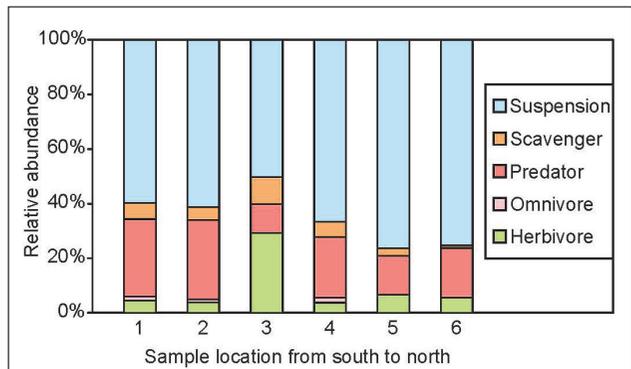


Figure 7. Relative abundance of gastropod feeding habits by sample. Suspension = suspension feeder.

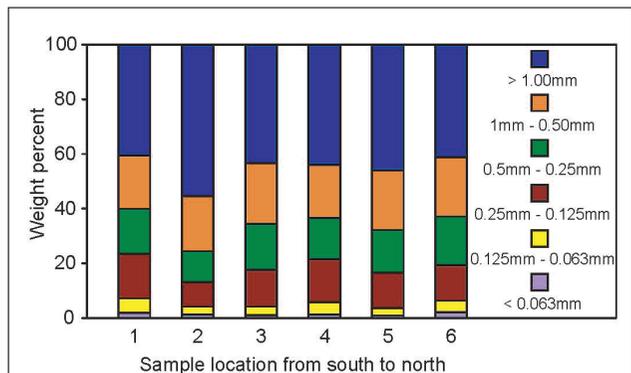


Figure 8. Sediment grain size distribution by sample.

for mollusks, bivalves, and gastropods ($p = 0.02, 0.03, \text{ and } 0.02$, respectively) and RF for mollusks and bivalves ($p = 0.03 \text{ and } 0.003$, respectively) (Fig. 7; Appendix A).

Discussion

Predation trace frequencies varied among the laterally equivalent, spatially distributed samples; with over one-third of between-sample comparisons being significantly different (Table 1), we could not conclude that a single sample would be a reasonable representative of the entire bed (Table 1, Figs. 9, 10, and 11). Furthermore, the variation in predation frequencies among samples did not follow a consistent spatial trend (Figs. 9, 10, and 11). Trace frequencies did not trend directionally, and more distant samples were not more likely to differ than closer samples. For example, Samples 4 and 3 were less than 100 m apart (Fig. 1), but mollusk DHF in Sample 4 was over three times greater than in Sample 3 (0.099 versus 0.025, respectively) (Fig. 9A). Among epifaunal bivalves, Sample 2, with the lowest RF at 0, was located between the samples with the highest RF (Sample 1 at 0.080 and Sample 3 at 0.085)

(Fig. 11D). It is not clear from predation trace frequencies alone whether the significant differences represent random spatial variation, or are rather driven by some other ecological variable. Below, we explore other potential explanations for the observed spatial variation.

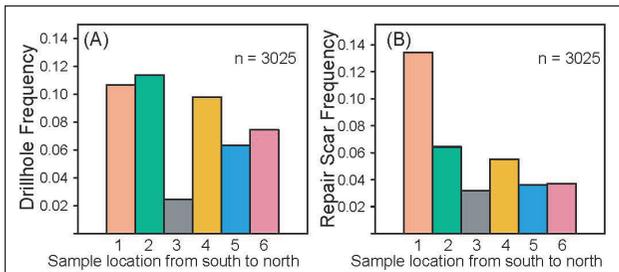


Figure 9. Predation trace frequencies on mollusks by sample. A. Drillhole frequencies. B. Repair scar frequencies. Samples from left (south) to right (north): 1 (peach), 2 (green), 3 (gray), 4 (yellow), 5 (blue) and 6 (pink).

Diversity metrics and generic abundances

There were no consistent patterns between diversity metrics and predation trace frequencies among the six samples, although it was noted that Sample 3 had the highest generic richness and the lowest predation trace frequencies for most categorizations (mollusk DHF and RF, gastropod DHF and RF, and bivalve DHF); but this relationship did not hold across the other samples. The one significant correlation among all diversity metrics and predation frequencies was between evenness and bivalve RF ($p = 0.003$); bivalve RF varied through the samples with the same rank order as evenness. Although it is possible that higher crushing predation on bivalves led to higher evenness among the entire sample, it is unlikely this is a causal rela-

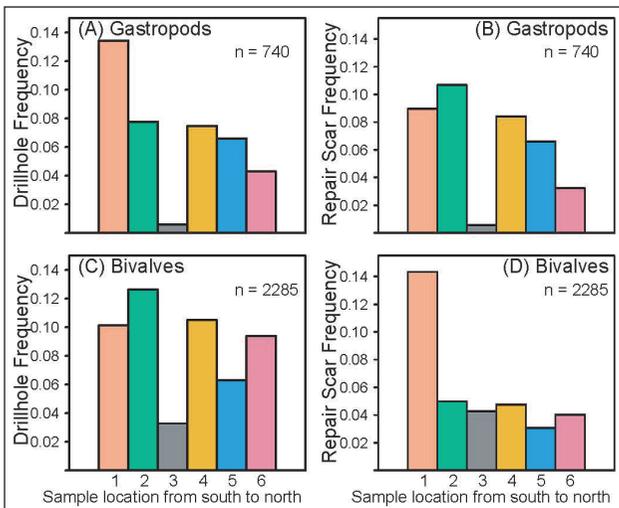


Figure 10. Predation trace frequencies on gastropods and bivalves by sample. A. Gastropod drillhole frequencies. B. Gastropod repair scar frequencies. C. Bivalve drillhole frequencies. D. Bivalve repair scar frequencies. Samples from left (south) to right (north): 1 (peach), 2 (green), 3 (gray), 4 (yellow), 5 (blue) and 6 (pink).

tionship. If repairs on bivalves led to higher evenness, then it would follow that higher repairs among gastropods or drilling among either group would demonstrate a similar pattern.

Abundant genera did not have higher predation trace frequencies than less-abundant genera, suggesting that predators did not prefer more available prey taxa. Our observations are consistent with Hansen and Kelley (1995), who found that certain preferred taxa were drilled at a frequency higher than their relative abundance in the assemblage. There is no evidence that predation on the highly abundant genera drove the overall predation trace frequencies.

Predator abundance

Predator abundance can be a predictor of predation trace frequency (Hansen and Kelley 1995, Stafford et al. 2015b). Very few potential predators were recovered in our samples (among drillers, seven individual muricid gastropods and one naticid gastropod; among predators that crush, peel, or chip prey shells, three busyco-

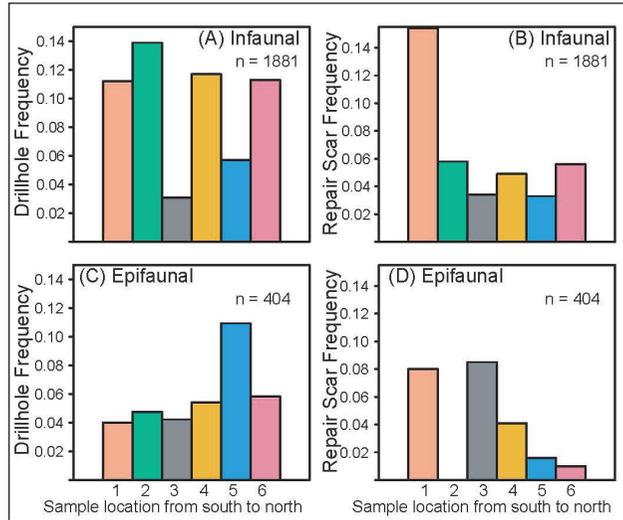


Figure 11. Predation trace frequencies on infaunal and epifaunal bivalves by sample. A. Infaunal bivalve drillhole frequencies. B. Infaunal bivalve repair scar frequencies. C. Epifaunal bivalve drillhole frequencies. D. Epifaunal bivalve repair scar frequencies. Samples from left (south) to right (north): 1 (peach), 2 (green), 3 (gray), 4 (yellow), 5 (blue) and 6 (pink).

Table 1. P-values for corrected Fisher's exact test comparing drillhole frequencies and repair frequencies between samples. Tests were performed for all mollusks, all bivalves, and all gastropods. Bold text indicates p-value < 0.05.

Drillhole Frequency, Mollusks

	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Sample 1	0.82	< 0.001	0.79	0.03	0.15
Sample 2	-	< 0.001	0.59	0.01	0.08
Sample 3	-	-	< 0.001	0.004	< 0.001
Sample 4	-	-	-	0.05	0.29
Sample 5	-	-	-	-	0.59
Sample 6	-	-	-	-	-

Drillhole Frequency, Bivalves

	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Sample 1	0.50	0.001	0.90	0.10	0.87
Sample 2	-	< 0.001	0.50	0.006	0.36
Sample 3	-	-	< 0.001	0.08	0.004
Sample 4	-	-	-	0.06	0.81
Sample 5	-	-	-	-	0.17
Sample 6	-	-	-	-	-

nine gastropods and a single crab claw, bearing molariform dentition), so the presence of predators can only be inferred from the occurrence of predation traces. Many of the drill-holes in the present study were likely of naticid origin (with a beveled edge; Carriker and Yochelson 1968), although many drilled prey were too small and thin-shelled for the trace maker to be determined. Potential muricid drillholes (straight-walled) were also identified. The presence of repair scars implicates any of a variety of shell crushing or peeling crustaceans, busyconine gastropods (Dietl 2003), as well as other predators (Stafford et al. 2015a and references therein).

Table 1. Continued.

Drillhole Frequency, Gastropods

	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Sample 1	0.40	< 0.001	0.40	0.38	0.06
Sample 2	-	0.01	1	0.92	0.40
Sample 3	-	-	0.01	0.02	0.10
Sample 4	-	-	-	1	0.40
Sample 5	-	-	-	-	0.52
Sample 6	-	-	-	-	-

Repair Frequency, Mollusks

	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Sample 1	0.003	< 0.001	< 0.001	< 0.001	< 0.001
Sample 2	-	0.05	0.72	0.11	0.14
Sample 3	-	-	0.13	0.81	0.81
Sample 4	-	-	-	0.23	0.31
Sample 5	-	-	-	-	1
Sample 6	-	-	-	-	-

Repair Frequency, Bivalves

	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Sample 1	< 0.001				
Sample 2	-	0.90	1	0.47	0.87
Sample 3	-	-	0.99	0.71	1
Sample 4	-	-	-	0.49	0.87
Sample 5	-	-	-	-	0.87
Sample 6	-	-	-	-	-

Repair Frequency, Gastropods

	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Sample 1	0.86	0.01	1	0.78	0.20
Sample 2	-	0.002	0.80	0.50	0.05
Sample 3	-	-	0.008	0.02	0.23
Sample 4	-	-	-	0.86	0.20
Sample 5	-	-	-	-	0.40
Sample 6	-	-	-	-	-

Additionally, drilling and crushing/peeling are not the only modes of predation that mollusk prey face. Research by Geary et al. (1991), primarily examining material from the Pinecrest beds, suggested that stomatopod predation could be prevalent on gastropods. They estimated frequencies comparable to the repair frequencies found in the present study, although their gastropod specimens were mostly much larger (> 10 mm shell height) than those in our study. Hole-punching behavior (also observed among some crabs; Turra et al. 2005) could be considered crushing predation, but it is unlikely to result in repair scars as identified in this study (and no potential stomatopod holes were identified in our samples).

Unfortunately, the lack of preserved predators in the samples means that it is impossible to link the variation in predation trace frequencies directly to variation in the predator populations (in terms of predator identities, abundances, size, or age, etc.).

Environment and Ecology

Physical and biotic environments may also influence predation frequencies. The samples collected for this study span a distance of 700 m; not enough to expect latitudinal or climatic variation, but local variation in habitat or microhabitat (e.g., substrate, temperature, nutrients, etc.) is plausible.

Grain size analysis reveals consistently sandy substrates among the sample sites, and there was no correlation among grain size and predation frequencies (Fig. 8; Appendix B). This does not rule out the possibility of variation in other aspects of the environment, or the ecology of the living community not reflected in the substrate grain size.

Because different organisms have different environmental requirements and preferences, variation in taxonomic makeup, life modes, and feeding strategies may also reflect variation in microhabitats and/or nutrient availability among the samples (Figs. 4, 5, 6, and 7). Additionally, organisms with different lifestyles are not equally exposed or vulnerable to predation. We explored these variables for potential explanations for variation in predation trace frequencies.

The only variable that consistently correlated with trace frequencies at different taxonomic levels (except bivalve RF) was the relative abundance of predatory gastropods. The reason for this correlation is unclear, as predatory gastropods that drill or chip shelled prey are uncommon in the samples (across all samples, only seven muricid and one naticid drilling gastropods and three shell-chipping busyconine gastropods). At such low numbers, it is impossible to tell if the abundances of these gastropods in the community also correlated with trace frequencies. It may be that another unidentified variable drives both overall predatory gastropod abundance and trace frequencies.

Sample 3 differed the most from the other samples in DHF (Fig. 9, 10, and 11, Table 1). Although there are few correlations to suggest a consistent relationship between drilling predation and other variables, it may be informative to explore potential reasons why this particular sample differed from the others. The large number of herbivorous gastropods and suspension feeding bivalves in Sample 3 may indicate a higher concentration of *Thalassia* seagrass; Petuch's (1982b) examination of the Pinecrest beds noted that the overall fauna in Unit 7 may reflect a *Thalassia* environment. Miller (1988) similarly found that certain mollusks are indicative of a seagrass environment. Suspension feeding gastropods dominated the gastropod assemblages (Fig. 7), followed by predatory gastropods (Samples 1, 2, 4, 5, and 6) or herbivorous gastropods (Sample 3). Sample 3 differed from the other samples in that suspension feeding gastropods were relatively less common and herbivorous gastropods relatively more common. This coincides with lower DHF and RF among gastropods in Sample 3. However, it is difficult to conclude that the low predation trace

frequencies are related to the distribution of feeding strategies, as only one drillhole and one repair scar were observed among all Sample 3 gastropods (on a suspension feeding and herbivorous gastropod, respectively). The low relative abundance of predatory gastropods in Sample 3 (Fig. 7) could be linked to the low DHF seen in both gastropods and infaunal bivalves in that sample; however, drilling gastropods were extremely rare to absent in all samples. It also does not explain the low RF of Sample 3 gastropods (as predatory gastropod abundance should have no direct effect on RF, although crushing predation can affect drilling frequency [Chattopadhyay and Baumiller 2010, observed in Plio-Pleistocene assemblages from Florida and other locations] or the low DHF in Sample 1 epifaunal bivalves [as predatory gastropod abundance was high compared to the other samples]).

Another potential explanation for spatial variation in predation trace frequencies is differential taphonomy between shells with traces and those without. Differential transport of drilled versus undrilled bivalve shells, due to the hydrodynamic effects of the hole, has been observed in laboratory and field experiments (Chattopadhyay et al. 2013 and Lever et al. 1961, respectively). On the other hand, Molinaro et al. (2013) observed no differential transport of drilled gastropod shells in the lab. The presence of drillholes may also increase the susceptibility of shells to fragmentation (Roy et al. 1994, in the laboratory), preferentially removing drilled shells in areas where post-mortem damage is higher. However, Kelley (2008) found nonsignificant or equivocal taphonomic patterns in Plio-Pleistocene bivalves from Florida. It is less likely that repair scars would affect the transport or taphonomy of shells; Blundon and Vermeij (1983) found that the presence of repair scars on gastropod shells did not affect the force required to break the shell. Another potential bias is that preferential removal of certain taxa from an assemblage (due to transport or damage) can alter the assemblage-level drilling frequencies (Klomp maker 2009). The potential influence of taphonomy and transport on predation trace frequencies is a likely direction for future research.

There are no definitive relationships explaining the variation in predation trace frequencies among the six spatially distributed samples, some of which were only 100 m apart. The variation may be caused by interactions among many factors, as-yet unexplored factors, or even random chance. Regardless, our findings demonstrate that a single sample would not be sufficient to accurately represent the predation trace patterns of the entire bed. Fossil sampling for predation should be designed to capture and account for spatial variation, both to improve temporal interpretations and to explore spatial variability in its own right.

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