Taphonomy as an Indicator of Environment: Smuggler's Cove, U.S.V.I.

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INTRODUCTION

In recent years, taphonomy has become more prominent in the paleontological and sedimentological literature. The emphasis of studies that deal with the post-mortem history of fossils has switched from what is lost from an assemblage, to the information that can be gained from the condition of what remains (see Muller, 1979 for a detailed discussion). Biological hardparts have been studied for their responses to physical processes (Seilacher, 1973; Nagle, 1967; Driscoll, 1970), chemical conditions (Flessa and Brown, 1983), and biological processes (Cutler, 1987; Driscoll, 1970; Perkins and Tsentas, 1976) in laboratory and modern field settings. Comparative taphonomy, the study of differential fossil preservation (Brett and Baird, 1986), has been used in ancient settings to document sedimentation rates (Parsons *et al.*, 1988; Miller *et al.*, 1988). Few comparative studies have been performed, however, that document the variations in taphonomic characteristics among different physical regimes in a modern setting where physical processes can be documented.

In the past, the reconstruction of paleoenvironments relied mainly on sedimentological characteristics (e.g. grain size, bed forms, or sedimentary structures) or on chemical features of the rocks. When fossils are used, environmental interpretation has been based solely on "taxonomic uniformitarianism" (Lawrence, 1971) where the habitat of a fossil's closest modern analog is assumed to have been the habitat of the fossil. This can be a rather flawed assumption since modern-day organisms are known that have changed habitat during their life history, and thus shifts in habitat can most assuredly occur over evolutionary time. Information on the taphonomy of fossils, however, is more directly controlled by the physical, chemical, and biological processes in the environment. Therefore, taphonomic indicators of environment can cross taxonomic boundaries and as a result, be more helpful in reconstructing paleoenvironments.

In the past, paleoenvironmental interpretations have typically been made on a gross scale based on major sedimentologic or taphonomic differences. This study attempts to test whether recognizable changes in taphonomic characteristics exist along a more subtle modern environmental gradient. If it can be demonstrated that the condition of molluscs from modern environments in Smuggler's Cove, a rather uniform, low-energy reef and lagoon system, reflect environmental differences, then the method will likely have usefulness in the ancient. Taphonomy can then be applied first to fossil assemblages from well-defined environmental settings, and finally to rocks that are more difficult to interpret using sedimentology alone (e.g. mudstones).

The work described below is part of a Ph.D dissertation underway at the University of Rochester. In that study twelve taphonomic characteristics that are possible indicators of biostratinomic processes are being evaluated in a number of modem carbonate environments. This paper discusses nine of these, measured in six different reef-related environments in Smuggler's Cove on St. Croix; characteristics include abrasion, color loss, articulation ratios, presence of sponge borings, ligament remains, live-dead ratios, microborings, gastropod borings, and percent cover by epibionts. These characteristics are probable indicators of overall physical energy of the sample location, as well as the biological activity in the area. Grain size, vegetation density, and current regime were also determined for each environment in order to document physical factors that might influence environmental differences. The usefulness of the nine taphonomic characteristics as possible indicators of environment (i.e. how well they reflect energy and biological activity) is discussed, as well as the projected usefulness of taphonomy in the fossil record.

METHODS

The study area is located in Smuggler's Cove on the north side of St. Croix. The samples were collected along a transect (Fig. 1) starting on Smuggler's Cove beach and continuing NNE across a mid-lagoon patch reef and over Tague Reef, a bank-barrier reef located 750 m from shore. The bottom characteristics along the transect vary from dense *Thalassia* beds near shore, to barren sand in the backreef, to cemented hardground on the patch reef and barrier reef (Table 1). Depths at sample sites range from 1 m at station SC1 to 10 m in the forereef (Table 1). Maximum depth along the lagoonal transect is 6.5 m.

All samples were collected with an airlift powered by a SCUBA tank. Samples were collected from the top of the airlift in a mesh bag with 5-mm holes. In sandy areas, a bucket with the bottom cut out was used to support the sides of the sample pit. Sediment was processed to varying depths depending on the cohesiveness of the sediment below. In hardground areas, samples were collected within the confines of a 25-cm^2 quadrat, and sand was vacuumed until the hardground surface was bare. The volume of sediment processed at each site was recorded (Table 1). Samples were rinsed, dried and sorted. All mollusc remains were separated from others (e.g. coral) noting live and articulated specimens, and then sieved at -2 phi, and the larger fraction was retained for laboratory analysis.

In the laboratory the samples were analyzed under a dissecting microscope at 10x power. Each specimen was identified to species level where possible. Bivalve shells were identified as left or right valves, and it was noted whether any ligament was present. All shells were compared to a standard and rated on a scale of 0 to 3 for amount of mechanical and biological abrasion. Mechanical abrasion includes wear from rolling in sand or gravel, resulting in the smoothing of sharp edges and wearing down of ornamentation (Driscoll, 1967); biological abrasion is considered here as algal microborings which leave fine-branching etch marks on the shells. The amount of breakage a shell had undergone was tabulated; breakage was recorded as none, minor or major. Minor and major breakage categories were divided further into the categories of 'fresh broken surfaces' and 'worn or encrusted broken surfaces' as an indicator of relative time since breakage. Color loss was rated on a scale from 'none' to 'high' (0-3). Presence/absence of gastropod borings, clionid sponge borings, and root etchings were also noted. And finally, the percent of surface area covered by epibionts was estimated. Epibionts included encrusting forams, tube-forming worms, and crustose coralline algae. Percent coverage on bivalves was determined for the interior and exterior of each valve, while for gastropods, coverage was estimated separately for spire, body whorl, and interior/aperture. Percent coverage was measured using a chart much like the percent area comparison charts used in petrography (Pichon, 1978).

Abrasion, color loss, and percent epibiont coverage were analyzed using Principal Components Analysis to evaluate the differences among environments and to determine which characteristics, if any, were the most reliable indicators of environment. These data were reserved for the multivariate method because they were analyzed along a continuous arithmatic scale and met the assumptions of the test. The other categories (e.g.

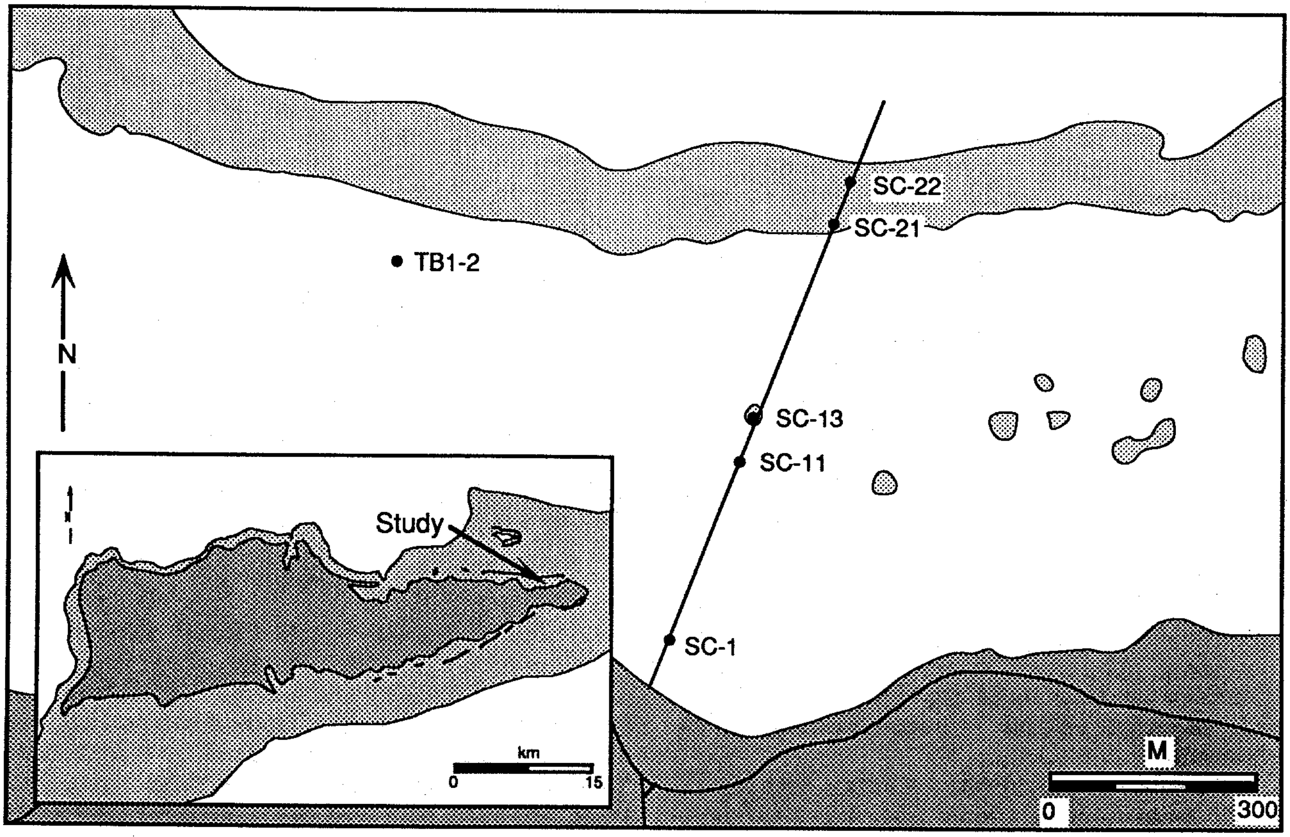


Figure 1. Location map for Smuggler's Cove showing transect and sample sites.

Table 1. Physical properties of the six sample localities. Sample sizes collected from each site are also included.

Locality	**Locality**	**Depth**	**sample size**		**Grain size**	**Grain**	**Current**	**Current**	**Seagrass**
Number	**Description**	**(m)**	**biv.**	**gast.**	**Mean (phi)**	**Sorting**	**Velocity**	**Direction**	**Density ††**
SC1	**Nearshore**	**2.4**	**23**	**30**	**2.11**	**1.25**	**4.2 cm/s***	**280°**	**116**
SC11	**Inactive Shrimp mds.**	**5.3**	**12**	**45**	**2.51**	**1.03**	**14 cm/s****	**240°**	**67**
TB1-2	**Active Shrimp mds.**	**5.5**	**36**	**14**	**2.46**	**1.10**	**ND**	**ND**	**30**
SC 13	**Patch Reef**	**2.5**	**191**	**55**	**0.63**	**1.48**	**11.6 cm/s*** 4.3 cm/s†**	**270°**	**0**
SC21	**Backreef**	**1.5**	**31**	**61**	**1.22**	**1.45**	**4.0 cm/s†**	**275°**	**0**
SC22	**Forereef**	**4.6**	**36**	**41**	**1.17**	**1.33**	**1.2 cm/s†**	**232°**	**0**

ND = no data
* Feb 23, 1989, calm day, strongly influenced by wave surge; method: Fluorescein dye
** Feb 17, 1989, 1 day after storm passed; method: 2m drogue
*** Feb 15, 1989, storm (45 mph winds); method: Fluorescein dye
† July 3, 1989, calm day; method: Fluorescein dye
†† Grass plants per 625 cm^2

gastropod borings, live/dead, left/right valves) were all based on a binary presence/absence scale and were analyzed graphically using sample means.

Environmental Characterization

Ambient currents were measured using fluorescein dye placed in the water column one meter above the bed and timed over a distance of three meters. In addition, a study of the currents of Smuggler's Cove was made just after a moderate storm passed, using drogues suspended 1 and 2 m below the water surface. Sediment samples were collected at each sampling site with a 30 cm3 piston core. Sediments were dried and seived at half-phi intervals, according to Folk (1974) to arrive at a sample mean and sorting value (Table 1).

The characteristics of the vegetation at each sample site were documented by identifying grass types and counting the number of blades/plants of *Thalassia testudinum* and *Syrengodium filiforme*. A 625 cm^2 quadrat was thrown haphazardly at the sample site several times and the number of plants of each grass type in each quadrat was recorded. These two grasses often occur together in mixed stands, so the numbers were combined and averaged for each sample site (Table 1).

RESULTS

Multivariate Analysis

In the Principal Components Analysis (PCA) of the bivalve measurements (265 shells), component 1 (PC1) accounts for 84% of the variance in the data set, and together with PC2, 92% of the variance is explained (Table 2). Epibiont cover (interior and exterior) and color loss are the most important factors contributing to the first component (Table 2). PC2 rates epibiont coverage on the exterior of shells as negatively correlated to coverage on the interior of the shells. This could be a positioning variable; once epibiont growth begins on one side of the valve, chances. are it will not be infested as heavily on the opposite side. Figure 2 is a plot of the individual shells on the first two principal components, the epibiont component, PC1, and the positioning component, PC2. The samples collected from sand-bottom sites generally plot in the upper left corner of the graph while those from the hardground sites group towards the right. The lower left to upper right diagonal groupings are an artifact of the predominance of whole numbers in the data seta

An equivalent Principal Components Analysis could not be performed on the gastropod data because many of the shells had missing parts (e.g. the spire was broken off), and PCA could not be performed with gaps in the data. The spire data probably contribute significantly to the differences in taphonomic characteristics between environments because the spire is the part of the shell exposed to environmental conditions for the greatest amount of time. Therefore, it does not seem practical to ignore it. The raw data for gastropod epibiont cover were graphed, and are discussed below. Both bivalve and gastropod data were combined to arrive at mean values for

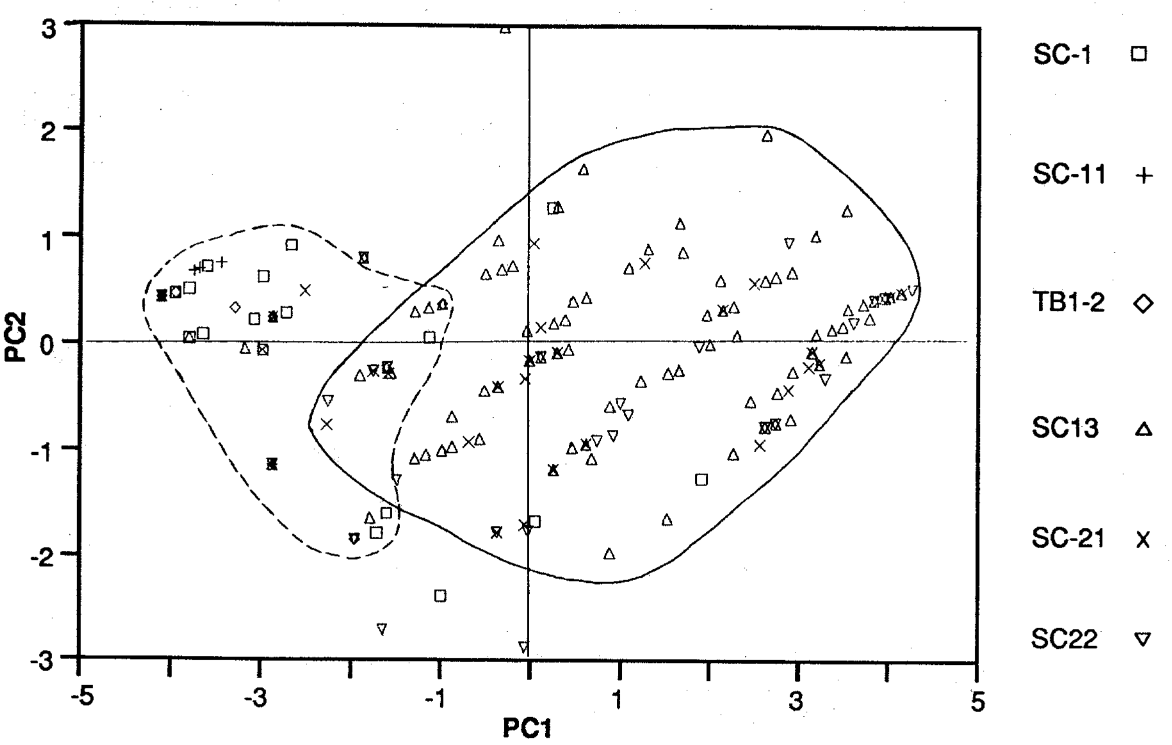


Figure 2. Plot of the 265 bivalve shells used in the Principal Components Analysis against the component scores of PC1 (epibiont cover) and PC2 (exterior vs. interior cover). The region occupied by the majority of sand-bottom specimens is outlined with a dashed line while the region with the majority of hardground specimens is marked with a solid line. The backreef speciments (X's) are almost evenly distributed with respect to these two components.

abrasion, color loss, breakage and borings. These were plotted to show, in a general way, what differences exist between environments.

Abrasion (Fig. 3) - The three hardground areas (SC13, SC21, and SC22) exhibit considerably higher levels of abrasion than the three sand-bottom areas (SC1, SC11, and TB1-2). In general, levels of biological abrasion were higher than mechanical abrasion. This probably reflects the low-energy level in Smuggler's Cove which leave shells exposed and generally undisturbed. Instead of becoming worn due to physical energy, they are attacked by microboring organisms.

Mechanical abrasion results from movement of the shells on the substrate. Shells on hardgrounds are exposed to current and wave activity for longer periods of time, and therefore, hardground samples tend to display greater mechanical abrasion. Table 1 summarizes current activity along the transect under a variety of wave regimes. The strongest non-storm currents occur at the backreef, patch reef, and nearshore sites. Storm readings tend to be an order of magnitude higher than those on a calm day. It is difficult to say whether or not day-to-day 2-4 cm/sec currents have any abrasive effect on shells. It is more likely that wave action at the shallow sites contributes more to the abrasion of the shells, and that currents are significant only when they are greater than 10-20 cm/sec. During calm weather, then, most mechanical abrasion results from the back and forth motion of waves feeling bottom, which implies that the highest abrasion levels will occur in the shallowest areas. This holds true for the hardground sites and may be a good distinguishing feature among the hardground environments.

Related to abrasion is the mean grain size of sediments at each site. As grain size increases, the abrasive affects also go up (Driscoll, 1967). The coarsest sediment occurs on the patch reef (0.63 mm; Fig. 3b) where mechanical abrasion was found to be greatest. Therefore, ambient energy conditions (reflected in large

***Table 2**. Eigenvectors and eigenvalues for the Principal Components Analysis of* 265 *bivalves.*

Original Variables	PC 1	PC2
mechanical abrasion	0.353	0.023
biological abrasion	0.874	0.055
color loss	1.029	0.183
interior epibiont coverage	1.812	0.447
exterior epibiont coverage	1.780	-0.593
% of total variance explained	86.082	6.026

grain size) combined with depths within wave base result in more highly abraded shells.

Biological abrasion (algal microborings) is lowest at site TB 1-2, a zone of active *Callianassa* mounds (Fig. 3a). Shells collected at this site were largely buried and thus not exposed long enough to allow the microboring organisms to settle. The frequency of microborings is greater at the nearshore site, probably due to periodic reworking by waves, which would expose the shells to microborers. The highest mean cover by microboring organisms was found in the backreef, but no significant differences were found between any of the three hardground sites. The means at the nearshore site, the area with the highest occurrence of microborings for the sand-bottom sites, and the patch reef, which had the least of the hardground sites, were compared using a t-test and found to be significantly different ($p \leq 0.05$).

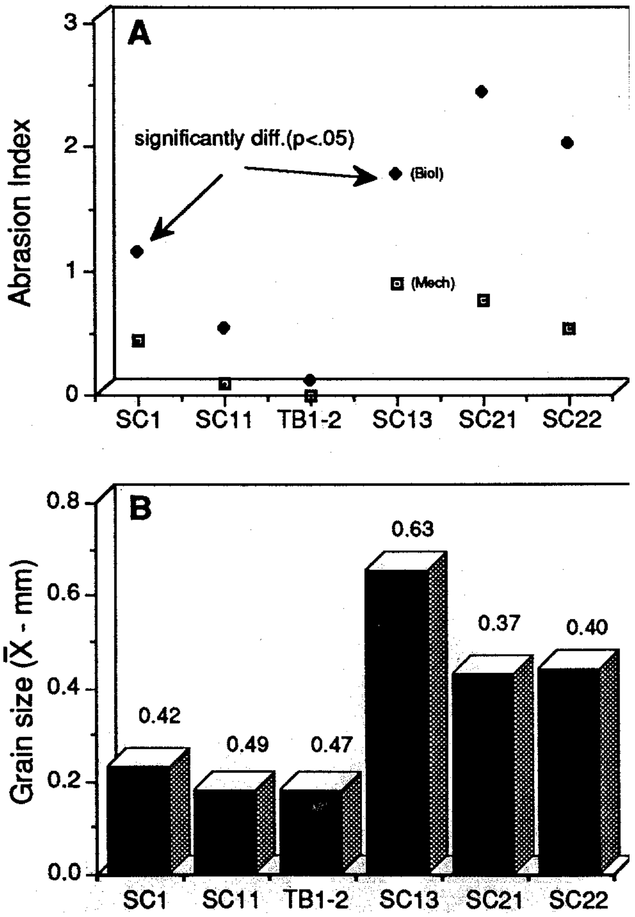


Figure 3. *Mechanical and biological abrasion of shell surfaces. A. Differences in biological abrasion were signficant for separating hardground areas from sandy areas ($p < .05$). Though there appear to be differences in the amounts of mechanical abrasion between environments, these were not found to be significant. Sample size = 538 shells. B. Grain-size distribution across Smuggler's Cove. Note that the patch reef has the highestmean grain size as well as the highest degree of mechanical abrasion.*

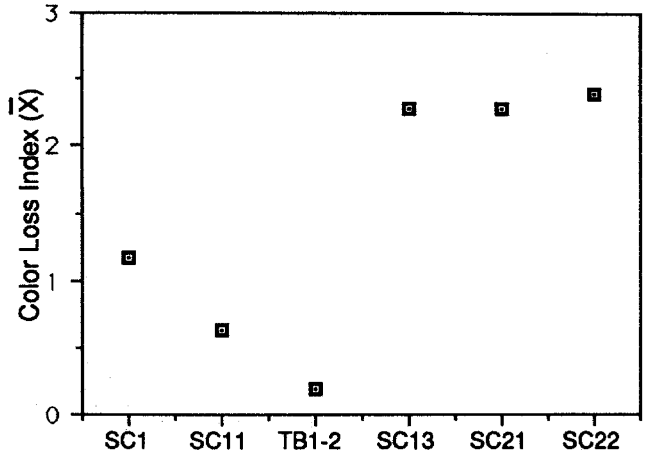


Figure 4. *Color loss was greatest in the hardground samples. Differences in color loss may help in subdividing the modern sand-bottom sites (SCI, SC 11, and TB1-2) because losses seem to increase toward shore (SCI). $n = 538$.*

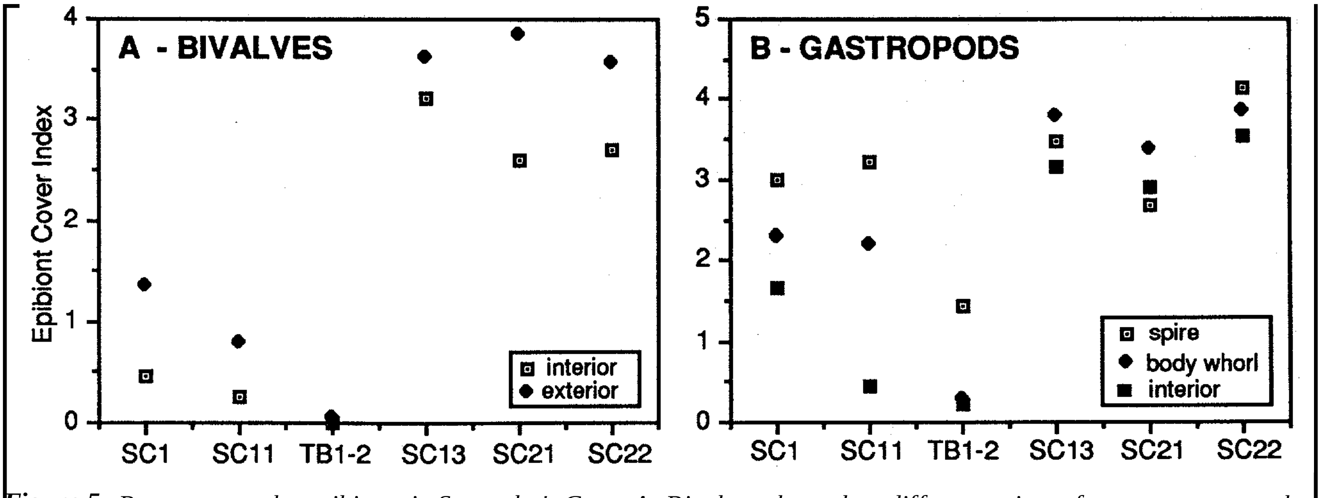
Color loss (Fig. 4) - The loss of color occurs when the outer layers of the shell are either abraded off, or the colors simply fade with time. Color loss is higher on average on the hardground substrates than at sand-bottom sites. This likely reflects the difference between exposure and burial. Colors seem to be lost relatively quickly, however, so this characteristic may not be very useful in the fossil record.

Epibiont coverage (Fig. 5) - Percent cover by epibionts was split into bivalves and gastropods. There were almost no epibionts on the bivalves from the site with active *Callianassa*, compared to about 15% cover in the nearshore sample. This can be attributed to a lack of exposure at the sediment/water interface where most encrusting organisms are active. The hardground bivalves averaged nearly 60% cover, and distinguishing among the three hardground areas is not possible on the basis of these data.

Epibionts on gastropods from sandy sites are more abundant than those on bivalves from sandy sites, which is a result of the burrowing nature of most bivalves, compared to gastropods in the grassy areas, which live at the surface. Coverage was consistantly high on the spire in gastropods across all environments. The spire is the oldest part of the shell and thus has the best chances for becoming encrusted. Epibionts will settle on the spire of ceriths, which are common grass-bed snails, as they graze on encrusting epibionts on blades of *Thalassia*. Interestingly, encrustation may cease when the snail dies if it is buried in the sand. Therefore, in grassbed dwellers, encrustation may reflect the amount of time a mollusc lives at the surface, whereas on the hardgrounds, encrustation is more an indicator of time since death.

Other taphonomic characteristics

Breakage (Fig. 6) - The amount and type of breakage that the shells undergo is a function of the physical energy



igure 5. Percent cover by epibionts in Smuggler's Cove. A. Bivalves show clear differences in surface-area coverage by epibionts. Shells from the three hardground sites (SC13, SC21, and SC22) had much more cover than those from the sand-bottom sites (SCI, SC11, and TB1-2). B. Differences were not as clear in the gastropods, but substrate type is distinguishable. Spire coverage is consistently high across environments except the active Callianassa *site (TB1-2).*

of the environment, the life history of the organism, and also the shape, size, and thickness of the shell itself. The sample with the lowest percentage of broken shells (TB 1-2; 28%) was from an area of active callianassid shrimp mounds (Fig. 6a). The majority of shells at site TB 1-2 were small, thin-shelled tellins. Tellins are burrowing clams that have most likely never been exposed to surface processes. Whatever breakage they have undergone is probably due to bioturbation caused by the burrowing of other clams and by the shrimp *Callianassa.* All of the sand-bottom samples had a lower percentage of broken shells than the hardground samples. The locality with the most broken shells, on the other hand, was the backreef (SC21, 87%), although the patch reef and the forereef had similar amounts of breakage (84% and 85% respectively; Fig 6a).

Shells at the surface undergo several episodes of breakage as they are moved by waves and bottom currents. The degree to which those broken surfaces are worn or encrusted with epibionts is an indicator of the time since the breakage occurred. Figure 6b compares fresh breaks with worn broken surfaces. Shells with fresh breaks are most common in the sand-bottom areas, and of those, the *Callianassa* mound site has by far the most shells with freshly broken surfaces. Shells with worn broken surfaces are more common in the hard grounds, but no further differentiation of hardground environments can be made on the basis of fresh vs. worn surfaces. A high percentage

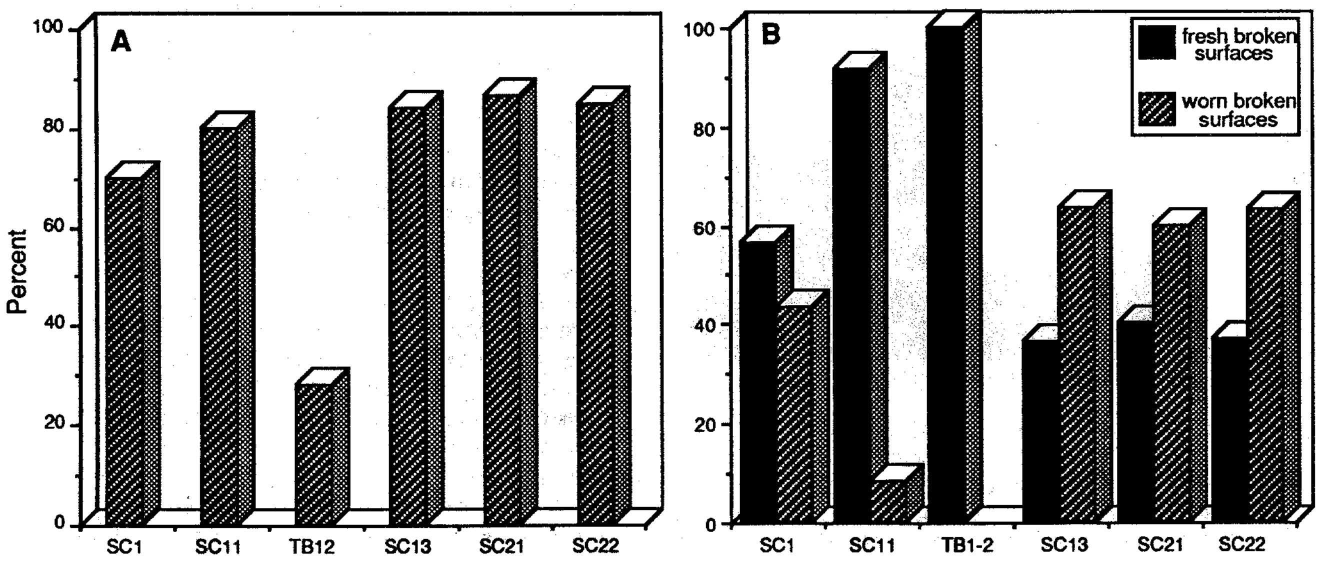


***Figure 6**. Breakage of molluscs A. Breakage is highest at all three hardground sites. The sample with the lowest percentage of broken shells is the site with active* Callianassa *shrimp mounds. B. Fresh broken surfaces predominate in the sand-bottom assemblages while worn surfaces were more common on the hardgrounds.*

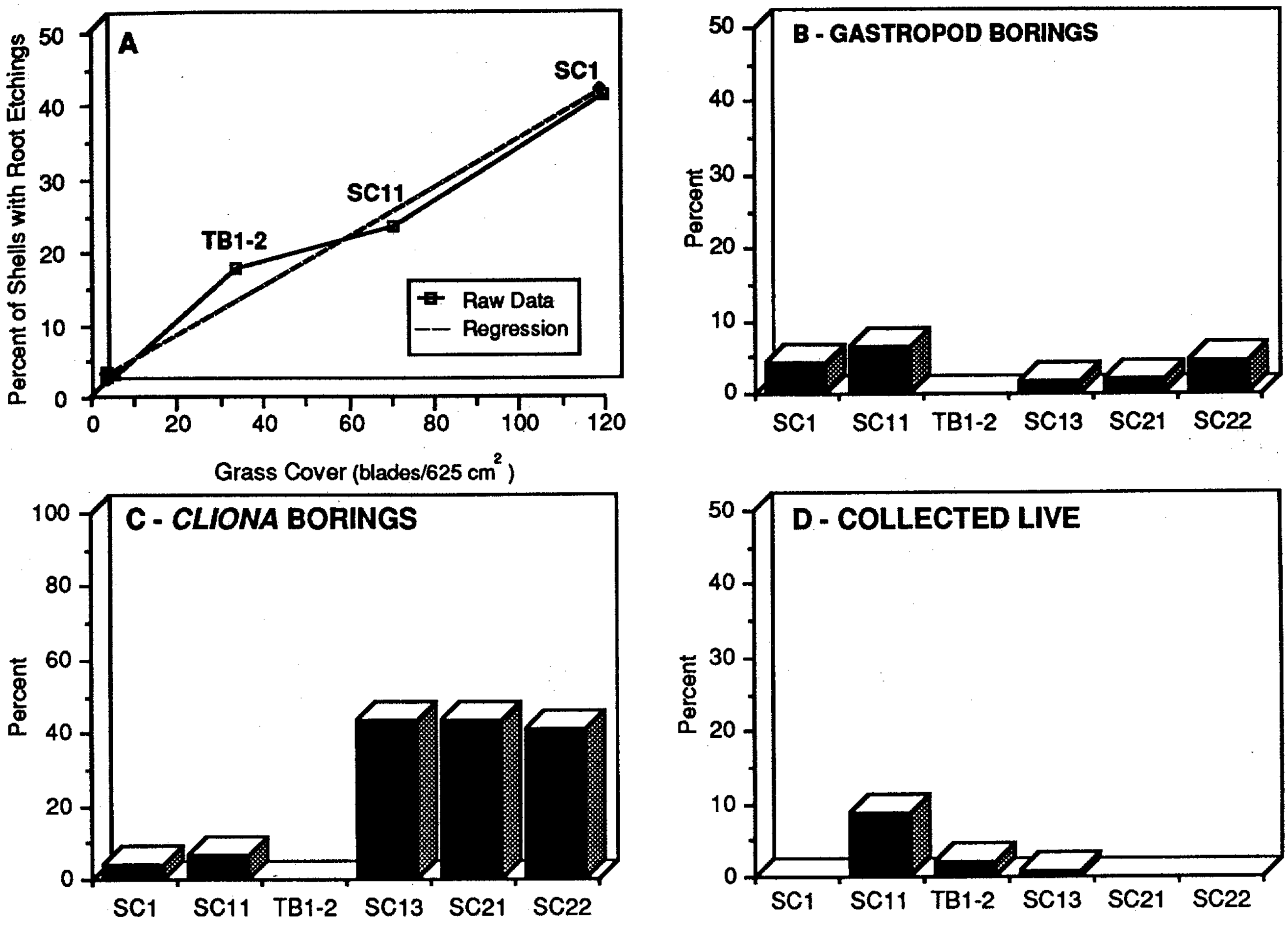


Figure 7. *A. The distribution of shells with root etchings plotted against sea grass density. There is a significant correlation between root etchings and the density of sea grass (p<.01). B. Importance of gastropod borings. Shells with gastropod borings are fairly evenly distributed across environments, although they are absent at site TB1-2. C.* Cliona *borings in mollusc shells. Shells with borings by the sponge Cliona are common on the hardground environments. Note that scale is different on this graph. D. Percent of shells collected alive. Few shells were collected live, and those that were came only from mid-lagoon sites.*

(58%) of shells with broken surfaces in the nearshore environment were worn, which can be attributed to wave activity, leading to values approaching other wave-dominated zones such as the patch reef. Shells in the surf zone undergo repeated breakage and rapid abrasion of their broken surfaces as waves approach the beach.

Root etchings (Fig. 7a) - Shells recovered from grassy areas often have white, cloudy etchings produced by contact with seagrass rhizomes. The percentage of root etchings per sample was highly correlated with total grass cover along the transect ($p \leq .001$). It is interesting to note that shells on the patch reef and backreef have shown evidence of root etchings, although none appeared in this data set. This indicates that, at some point in time, they resided in a grass bed. Root etchings in hardground settings may be a good indicator of transport.

Gastropod borings (Fig. 7b) Predatory gastropods have the ability to drill through the shells of other molluscs and feed on the animal inside. These predators (e.g. muricids, naticids) leave a distinctive bevelled hole on their prey. The presence of borings indicates the presence of predatory gastropods, and residence of a shell at the sediment/water interface. Often borings were found in burrowing clams indicating that they were exposed, either by water motion or bioturbation, long enough to be attacked. The low frequency of gastropod borings in the samples does not allow conclusions about environmental differences to be drawn at this time.

Borings were most common on shells collected from the area of inactive shrimp mounds (SC11), a sand-bottom area with moderate grass cover. The next highest percentage of gastropod borings was found in the forereef sample. Overall, gastropod borings were not common at any of the sites, and completely absent in sample TB 1-2, from the area of active shrimp mounds.

Cliona borings (Fig. 7b) - Shells with galleries of the boring sponge *Cliona* were most common in the hardground samples. *Cliona* borings were present in low abundances in two of the lagoon samples, but completely absent from the site with active Callianassa mounds. *Cliona* borings, then, are a clear indicator of exposure of shells (hardground vs. sand), but are not very useful to further subdivide environments.

Shells collected live (Fig. 7d) - The mid-lagoon localities were the only samples with live specimens. Two of the sites (SC11 and TB1-2) are sand-bottom areas, while the third is the patch-reef site. Overall, there was a very small number of live specimens present in any of the samples. A small number of the bivalve specimens were collected as articulated specimens, indicating recent death. The ligament which holds the two valves together is a tough, durable fiber that tends to break apart in a matter of days after death of the clam. The nearshore sample contained 4 articulated bivalves, while the patch reef and the forereef each had one specimen. A larger percentage of single valves, however, had some traces of ligament still attached to the shell. This is a good indicator that the bivalve died fairly recently (days to weeks).

In the fossil record, the best-preserved shells have conventionally been the ones designated to have been alive at the time of burial. The taphonomic characteristics of these live, and very recently dead, specimens should reflect the least amount of alteration. This is not true for epibiont coverage, however. Many of the live specimens are already heavily encrusted.

DISCUSSION

Taphonomic characteristics appear to be a good general indicator of environment. However, subdividing the environments more finely than substrate type will require more detailed sampling from within each chosen environment. The most useful characteristics found so far in this study are epibiont cover, mechanical abrasion, the condition of the broken surfaces of shells, and the presence or absence of *Cliona* borings and microborings. Other characteristics, such as size of the shells and fragments of shells as well as type of epibionts should also prove to be helpful in further subdividing the environments. Data are presently being gathered to quantify these characteristics, but are not ready to be presented in this paper.

The true usefulness of any taphonomic characteristic lies in its ability to be recognized in the fossil record. A few, such as color loss, and mechanical abrasion (which can be easily confused with chemical dissolution during diagenesis) have limited value in the ancient. Mechanical abrasion may be useful where differences in energy levels are more dramatic (e.g. beach vs. lagoon). Epibiont coverage, which is a preservable feature, shows marked differences across Tague Bay, and therefore may be the most useful characteristic for separating paleo-environments.

In applying these data, it must be kept in mind that characteristics that are distinctive in a modem environment can be selectively removed or reduced due to chemical processes after burial, or mechanically removed during recovery from the rock in some fossil assemblages. Brachiopods preserved in mudstones, however, are known to have detailed preservation of worm tubes, encrusting corals, bryozoans, microborings, and edrioasteroids (Brett, 1983). Also, shells preserved as molds often leave remarkable impressions of encrusters as well as detailed infills of the galleries of macro- and microboring organisms. Ongoing research related to this study will take advantage of the moldic preservaton of shells in the reefs of the Blessing Formation on St. Croix to test the subdivision of environments based on the taphonomic criteria established in the modern.

Taphonomic features of shells are unique in that, for the most part, they are recorded in the shell both during life and after death, until the time of final burial of the shell. Some features, such as breakage, occur primarily after death of the organism. These features are a reflection not only of physical processes, but a combination of physical, chemical, and biological processes that together constitute the "fingerprint" of a specific environment.

Such taphonomic signatures can be complicated by transport of a shell from one environment to another, which will mix the signals of two environments if the shell remains in the second environment for any length of time. However, shells that are transported out of their original environment are often moved by processes strong enough to cause their immediate burial. This results in a misplaced, but intact environmental signature. Alternatively, the result can be two mixed assemblages which could be detected by bimodal distributions in the data.

In Smuggler's Cove, it was assumed that the samples collected for this study were in-place assemblages and thus representative of their environment. Flume studies performed in the field in Smuggler's Cove indicate that instantaneous velocities up to 120 cm/sec were not sufficient to move sediments in the grass beds (D.K. Hubbard, pers. comm.). A 3-m, 10-sec. wave in 3 m of water would have U_{max} at 1 m above the bed of only 93 cm/sec. Therefore the assumption that transport is unlikely appears valid for the lagoon samples (it should be noted, however, that hermit crabs may cause some mixing of gastropod assemblages). The preceding paper by Miller (this volume) shows that the spatial variability of lagoon shell assemblages is clearly the result of habitat differences (grass cover) and not post-mortem transport.

For the most part, taphonomy was found to be a reliable indicator of hardground vs. sand bottom. Within sandy environments, it was fairly reliable in singling out the *Callianassa* mound assemblages. The hardground subenvironments were not easily discerned from the available data, but with more detailed surveys, (including size of shell fragments and type of epibionts on the shells), the hardground subenvironments may show more distinct taphonomic differences.

CONCLUSIONS

1) The relative amounts of epibiont coverage, breakage, macro- and microborings, and abrasion are useful indicators of the post-mortem environment of shells in Smuggler's Cove.

2) The condition of the shells is a result of the physical and biological processes acting in that environment.

3) Environmental energy, and thus faunal mixing, in Smuggler's Cove near-surface samples is low.

4) Therefore the criteria found most useful here, are likely related to variations in the environments identified at Smuggler's Cove, and can be applied with relative confidence to similar ancient assemblages.

ACKNOWLEDGEMENTS

Financial support was provided by GSA Grants in Aid of Research and The Roger Tory Peterson Society. Logistical support was provided by the West Indies Laboratory faculty, staff, researchers, and students. Numerous discussions with Carlton Brett, Dennis Hubbard, Judy Massare, and Peter DeCelles helped in formulating this project. Field work would have been slow at best without the help of Dennis Hubbard and Laura Venger.

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