

QUANTIFYING TAPHONOMIC BIAS IN MOLLUSCAN DEATH ASSEMBLAGES FROM THE UPPER CHESAPEAKE BAY: PATTERNS OF SHELL DAMAGE

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ABSTRACT

This study focuses on two main questions: (1) what types of shell damage occur in the death assemblage of upper Chesapeake Bay benthic mollusks; and (2) how does shell damage differ according to intrinsic factors such as life habit, shell mineralogy, and shell organic content. Extrinsic and intrinsic factors, ranging from the environment to shell composition, interact to influence the quality of fossil preservation. Our understanding of how extrinsic factors affect shell-damage profiles has improved dramatically with the development of taphofacies models, but the role that intrinsic factors play is still poorly understood. Molluscan death-assemblage material was obtained via box coring, identified, and assigned taphonomic damage states. The most common forms of shell damage were disarticulation, fine-scale surface alteration (FSA), periostracum loss, edge modification, and fragmentation. Four patterns were documented consistently across habitat types when shell damage was examined according to life habit and shell composition. Infaunal specimens exhibit significantly more severe damage due to internal FSA than epifaunal specimens. Calcitic specimens experience higher levels of external encrustation than noncalcitic specimens. Specimens with high levels of shell organics experience significantly more fragmentation and edge modification than specimens with low levels of shell organic content. The direction and degree to which other damage variables differ among intrinsic categories vary according to the variable assessed or the habitat type sampled. In the northern sites (i.e., deeper water), all the variables that recorded differential damage according to shell-organic content recorded greater damage in specimens with high shell organic content, suggesting that the latter may be experiencing selective removal from the death assemblage.

INTRODUCTION

The habitats and molluscan diversity that characterize Chesapeake Bay make it possible to explore to what extent intrinsic factors are affecting taphonomic damage, while at the same time controlling for extrinsic factors in the form of habitat type. Although taphonomic bias has been assessed in a handful of estuarine environments (Jackson, 1968; MacDonald, 1969; Zenetos, 1990, 1991), past studies rarely incorporate information on shell damage. The goals of this study are to: (1) survey the types of shell damage that occur in the death assemblage of bay benthic mollusks, and (2) determine whether shell damage in Chesapeake Bay mollusks varies according to intrinsic factors such as life habit, shell mineralogy, and shell organic content.

The quality of fossil preservation is controlled by extrinsic factors, which relate to the environment where specimens accumulate, and intrinsic factors, which relate to the original attributes of the specimens. Extrinsic factors include all the mechanical, biological, and chemical processes acting in a specific environment over a particular timescale. In-

trinsic factors include such biological traits of specimens as life habit, skeletal mineralogy, skeletal organic content, skeletal thickness, body plan, and behavior that influence their susceptibility to damage and preservation. During the past two decades, the importance of extrinsic factors has been emphasized repeatedly (for a review, see Cadée, 1991; Kidwell and Bosence, 1991; Best and Kidwell, 2000a). Indeed the concept of taphofacies analysis is predicated on the idea that, as a fossil assemblage develops, it passes through a taphonomic filter, leaving a distinct signature that can be used for paleoenvironmental reconstruction (Brett and Baird, 1986; Speyer and Brett, 1986; Davies et al., 1989; Meldahl and Flessa, 1990; Staff and Powell, 1990a; Kowalewski et al., 1994; Pandolfi and Greenstein, 1997; Best and Kidwell, 2000a). In contrast, the importance of intrinsic factors in the taphonomic equation (Kidwell and Bosence, 1991) has received relatively little attention until recently (Parsons and Brett, 1991; Parsons, 1993; Dent, 1995; Aguirre and Farinati, 1999; Best and Kidwell, 2000b; Kidwell et al., 2001; Nielsen and Funder, 2003; Lazo, 2004; Nielsen, 2004).

The life habit of an organism is thought to exert some control on shell damage, depending on exhumation cycles of shells in sediment (Cummins et al., 1986; Best and Kidwell, 2000b; Kidwell et al., 2001). Intuitively, epifaunal taxa should be more prone to most forms of damage, since they are more likely to be deposited postmortem above the sediment-water interface. Although microbial attack continues after burial, most types of damage occur exclusively or most rapidly above the sediment-water interface (reviewed by Kidwell and Bosence, 1991; Parsons and Brett, 1991).

Preservation potential of mollusks is also dependent on a variety of factors related to shell composition, including shell mineralogy, inter-crystalline organic content, and crystallite surface area to volume ratio (Currey and Taylor, 1974; Glover and Kidwell, 1993; Harper, 1998a; Clark, 1999; Harper, 2000; Kidwell, 2005). In general, aragonitic taxa are thought to be less likely to be preserved in the fossil record than bimineralic or calcitic ones (Harper, 1998b). Organic content likewise plays a role in the long-term stability of shell material (Glover and Kidwell, 1993). In the early stages of dissolution, the presence of organic matrix may temporarily protect mineral crystallites from damage, but over time organic matrix provides a substrate for microbial decay, ultimately promoting destruction of microstructure (Glover and Kidwell, 1993).

MATERIALS AND METHODS

A shell-damage survey was performed on four sites in the main channel of the upper bay (Fig. 1). The sites are distributed lengthwise in the upper bay and represent two distinct habitat types (Table 1). Sites 1 and 2, located in the northern portion of the upper bay, are characterized by seasonally variable salinities (2.7 to 15.2 ppt), high silt-clay ratios (92–95%), and moderate water depth (4.4–7.5 m). In comparison, the southernmost sites (3 and 4) record less variable salinity, sandier substrates, and shallower water depths (Table 1). The basic differences between these sites make it possible to control (very generally) for habitat type in these shell-damage analyses. Death-assemblage material was generously pro-

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¹ www.sepm.org/archive/index.html

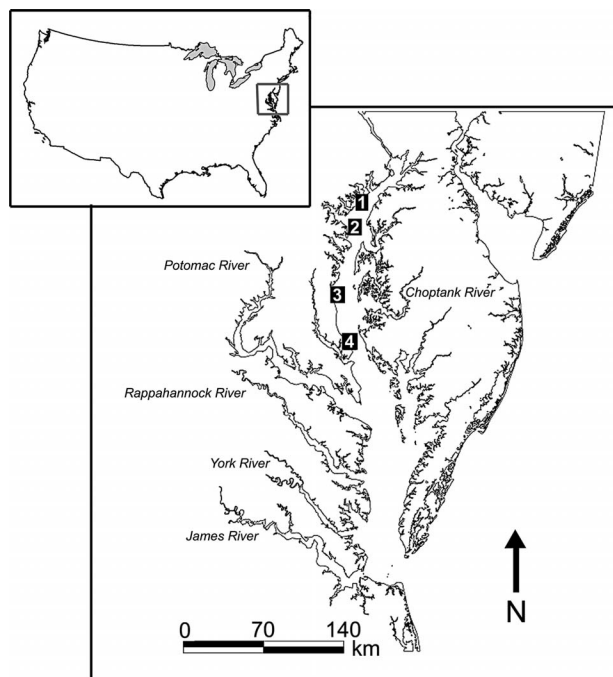


FIGURE 1—Map of the Chesapeake Bay (Atlantic coast, North America) illustrating the sites sampled in this study.

vided by the benthic monitoring division of the Chesapeake Bay Program (CBP; Diaz et al., 2003).

The CBP collected one to two samples at each site, in May or September of 2002, using Wildco and hand-operated boxcorers of similar size (VERSAR, 2002). Field samples were sieved to 0.5 mm and then preserved in a 10% buffered formaldehyde solution. Physical variables, including salinity, temperature, pH, dissolved-oxygen concentration, and sediment grain size, were collected for each sampling event. Twenty years worth of sedimentological and physical data were provided for each site by the CBP (VERSAR, 2002). In the lab, samples were gently resieved into four fractions (>4 mm, 4–2 mm, 2–1 mm, and 1–0.5 mm), rinsed in freshwater, and air dried. Molluscan material, including both whole shells and fragments, was picked and identified to species level whenever possible.

Identifiable shells and fragments were assigned damage states using a categorical scoring system developed and adapted from previous work (Davies et al., 1989; Kowalewski et al., 1995; Best and Kidwell, 2000a, 2000b; Kidwell et al., 2001). Data on seven variables summarizing taphonomic shell damage were collected using 10–40x stereoscopic magnification of internal and external shell surfaces (Table 2). Type of encruster (bryozoan, barnacle, worm, or oyster) or bioeroder (sponge, worm, or both) was noted. Disarticulation was assessed only in taxa with more than

TABLE 2—Damage variables and scoring systems used to assess shell damage in the death assemblage. Disarticulation was quantified only in taxa with more than one valve (i.e., bivalves). Periostracum loss was only scored for species with periostraca and was quantified as follows: 0 signifies that the shell has no periostracum loss (>80% of periostracum intact), 1 signifies that the shell has slight periostracum loss (50–80% of periostracum intact), 2 signifies that the shell has moderate periostracum loss (10–50% of periostracum intact), and 3 signifies that the shell has severe periostracum loss (<10% of periostracum intact). Internal and external FSA were scored using a similar scale: 0 signifies that the shell has no FSA, 1 signifies slight damage (a chalky or dull appearance), 2 signifies moderate damage (a chalky appearance and <60% of the shell pitted or eroded), and 3 signifies severe damage (a chalky appearance and >60% of the surface area pitted or eroded). Fragmentation was scored based on the size of fragment: 0 signifies no fragmentation (100% of valve), 1 signifies moderate fragmentation (large fragment, >20% of valve), and 2 signifies severe fragmentation (small fragment, <20% of the valve). Edge modification was ranked similarly: 0 signifies no edge modification, 1 signifies slight damage (chipped shell edge), and 2 signifies severe damage (rounded shell edge). Damage variable abbreviations: Enc = encrustation; Disart = disarticulation; Perio = periostracum loss; Bioero = bioerosion; FSA = fine-scale surface alteration; Frag = fragmentation; Edge mod = edge modification; Ext = external; Int = internal.

Variable	Position	States
Enc	Int/Ext	% surface
Disart	—	0 = absent 1 = present
Perio	Ext	0 = none 1 = slight 2 = moderate 3 = severe
Bioero	Int/Ext	0 = absent 1 = present
FSA	Int/Ext	0 = none 1 = slight 2 = moderate 3 = severe
Frag	—	0 = none 1 = <20% shell 2 = >20% shell
Edge mod	—	0 = none 1 = chipped 2 = rounded

one valve (i.e., bivalves), and periostracum loss was assessed only for species with periostraca. SEM (scanning electron microscope) inspection of shell surface features, which is generally required to distinguish chemical dissolution of crystallites, organic leaching, fungal or algal micro-boring, and physical abrasion (Cutler, 1995), was not feasible for this study. Therefore, these factors were combined into a single variable of fine-scale surface alteration (following Best and Kidwell, 2000a). Shell-damage states with internal scoring were assessed outside of the pallial line on the interior of the shell and only for bivalve specimens with identifiable pallial lines. Levels of fragmentation and disarticulation in this dataset may be artificially inflated due to detritus handling and

TABLE 1—Data on the sites sampled in this study. Data include number of samples collected, sample dates, number of specimens in the death assemblage, salinity, latitude (lat) and longitude (long), the percentage of silt-clay, the collecting gear, and the water depth (VERSAR, 2002). Note that Sites 1 and 2 (northern sites) are slightly deeper and have higher silt-clay percentages than Sites 3 and 4 (southern sites).

Site	# Samples	Sample dates	# Specimens	Salinity (ppt)	Lat Long	Silt-clay %	Gear	Water depth (m)
1	2	May 02	677	2.7	39°16.28'N	94.5	WildCo	4.4
		Sept 02	660	11.3	76°17.42'W	94.4	Box	4.5
2	2	May 02	51	9.9	39°07.32'N	95.2	WildCo	7.5
		Sept 02	184	15.2	76°21.34'W	92.5	Box	7.5
3	1	Sept 02	525	14.5	38°42.90'N 76°30.84'W	1.9	Modified Box	2.8
4	2	May 02	445	16.5	38°25.19'N	1.0	Modified	2.6
		Sept 02	670	14.9	76°25.02'W	1.2	Box	3

transport (Flessa et al., 1992); however, inspection of samples in the field and throughout lab preparation indicated that artifactual breakage was not substantial and should not affect the results significantly (see also Davies et al., 1989; Best and Kidwell, 2000a). Preservation of the shell material in formaldehyde by the CBP made it impossible to date the dead specimens via radiocarbon dating or amino acid racemization. It is unclear, therefore, to what extent shell age is influencing shell damage in these data.

The size of shells and shell fragments can exert significant influence over taphonomic signal (Kidwell et al., 2001). The use of multiple sieve sizes in this study makes it possible to assess the extent to which specimen size is affecting the results. Sample size does differ according to sieve size ($n = 542$ [>4 mm]; 762 [4–2 mm]; 1318 [2–1 mm]; 590 [1–0.5 mm]), suggesting that smaller sieve sizes will drive the results reported here. To explore the effects of sieve size on damage profiles, all analyses were performed: (1) across all sieve sizes and (2) across larger sieve sizes (>2 mm). The results of these two analyses were similar, except where noted. A table of species and the sieve fractions in which they occur is provided in the Supplementary Data¹.

Data on life habit were compiled from the literature, and specimens were divided into epifaunal versus infaunal categories (following Best and Kidwell, 2000b). Information on shell mineralogy and microstructure was assembled from a variety of sources (Taylor et al., 1969, 1973; Kidwell and Brenchley, 1996). Data on shell composition were readily available for most of the species represented in the upper bay dataset. In cases for which compositional data were lacking, data on specimens within the same genus or family were substituted, but only when data were consistent within that genus or family. Species were divided into two categories on the basis of shell mineralogy: (1) calcitic, which includes taxa with purely calcitic and bimineralic shells, and (2) noncalcitic, which includes taxa with purely aragonitic shells. Species were also divided into two categories on the basis of shell organic content: (1) low organic content, which includes taxa with cross-lamellar, complex cross-lamellar, homogeneous aragonite, and foliated calcite microstructures, and (2) high organic content, which includes taxa with nacreous, prismatic aragonite, and prismatic calcite microstructures (following Glover and Kidwell, 1993).

Whenever possible, field and lab sampling protocol followed recommendations by Kidwell et al. (2001) and Kowalewski and Hoffmeister (2003) for standardized procedures. Detailed descriptions of field and lab methodology are provided in Lockwood and Chastant (2006).

RESULTS

Patterns of Shell Damage

Data for each shell-damage variable were summarized in three different ways: (1) the percentage of specimens affected, (2) the mean damage score, and (3) the median damage score (excluding encrustation and bioerosion) across all sites. Parsons-Hubbard (2005) has argued that calculating the median for damage scores is more meaningful than calculating the arithmetic mean, given the discontinuous nature of damage scores. In the Chesapeake Bay, however, damage due to encrustation and bioerosion is so rare that calculating the median produces a zero result across all categories, including species, life habit, mineralogical, and shell organic content categories. Median damage scores were therefore calculated only for disarticulation, periostracum loss, FSA, fragmentation, and edge modification. It should also be noted that, for the two-state variables employed in this study (e.g., disarticulation and bioerosion), percentage and mean damage metrics yield identical results.

Percent, mean, and median damage metrics are statistically significantly correlated with each other across all damage variables. When summarized at the species level, analyzed via Spearman Rank, and adjusted for multiple comparisons, R_{13-17} ranges from 0.56 to 1.0; p ranges from 0.025 to 0.0000001 except for fragmentation mean vs. median score ($R_{17} = 0.45$, $p = 0.07$). The three metrics also yield very similar results for

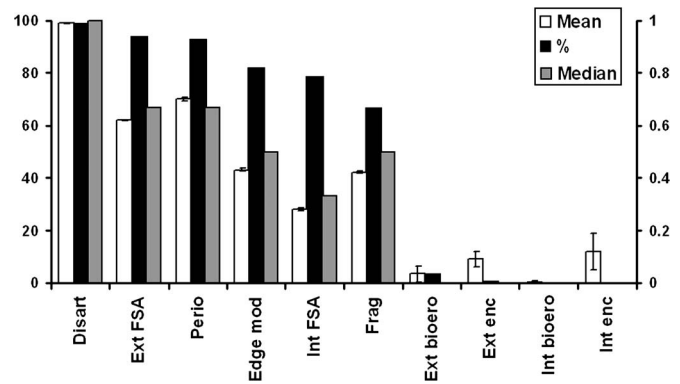


FIGURE 2—Data for each shell damage variable, compiled across all samples and sites. The data are summarized using three metrics: (1) percentage of specimens affected (0–100%), (2) mean damage score, and (3) median damage score. Mean and median damage scores are standardized from 0 to 1 to account for variables with varying numbers of damage states. Abbreviations for damage scores as in Table 2.

life-habit and shell-composition analyses; therefore, subsequent discussion will be limited to the results for mean damage scores.

Normality tests (Kolmogorov-Smirnov, Shapiro-Wilk's W) revealed that mean damage scores are not normally distributed ($d = < 0.53$, $p < 0.01$; $W = 0.83$, $p < 0.00001$), hence nonparametric statistics were used for subsequent analyses. Sequential Bonferroni adjustment was applied to each independent pool of statistical analyses (Rice, 1989).

The most common forms of damage (i.e., highest percentage of specimens affected, compiled across all samples and sites) recorded are disarticulation, external FSA, periostracum loss, edge modification, internal FSA, and fragmentation (Fig. 2). Encrustation and bioerosion are extremely rare in these samples (affecting $<4\%$ of specimens; Fig. 2). The most common encrusters are bryozoans, which cover 0–90% of specimen surface area, followed by worms (0–60%) and barnacles (0–35%). The most severe forms of damage (i.e., the highest mean and median) documented are disarticulation, periostracum loss, external FSA, edge modification, fragmentation, and internal FSA (Fig. 2). When these analyses are restricted to larger sieve sizes (>2 mm), the order of the most common and most severe forms of damage remains the same but the order of the rare forms (encrustation and bioerosion) is altered somewhat. Larger sieve sizes yield statistically significantly greater levels of external encrustation than smaller (<2 mm) sieve sizes (Mann-Whitney U test; $Z_{1896, 1283} = -3.54$; $p = 0.001$), but differences in bioerosion or internal encrustation are not statistically significant.

Scoring of internal versus external damage in three of the variables (encrustation, bioerosion, and FSA) makes it possible to compare the two approaches to assessing shell damage. All three external measures yield higher levels of damage (1.2 to 8.5x) than internal measures. Both encrustation ($R_{1654} = 0.65$, $p = 0.000001$) and FSA ($R_{1650} = 0.41$, $p = 0.000001$) record statistically significant correlations between internal and external measures of damage. Bioerosion does not ($R_{1655} = -0.002$, $p > 0.999$), although this is due primarily to the dearth of internally bioeroded specimens obtained in these samples ($n = 2$). These results did not change when analyses were limited to larger sieve fractions (>2 mm).

Effects of Intrinsic Factors: Data Pooled Across All Sites

Life Habit.—When specimens were pooled across all sites (overall analysis), Mann-Whitney U tests recorded significant differences between infaunal and epifaunal specimens for encrustation (both external and internal), periostracum loss, FSA (both external and internal), and fragmentation, after Bonferroni correction (Table 3). Epifaunal specimens display significantly higher levels of damage for external encrustation, internal encrustation, and fragmentation, while infaunal specimens display significantly higher levels of damage for periostracum loss, external FSA,

TABLE 3—Differences in mean damage score between infaunal and epifaunal specimens for the overall analysis and for each habitat type analysis. Differences are assessed using Mann-Whitney U tests and results (after Bonferroni adjustment) are provided. Abbreviations for damage scores as in Table 2. Positive Z values denote greater damage in infaunal relative to epifaunal specimens. Negative Z values denote greater damage in epifaunal relative to infaunal specimens. The number of asterisks denotes the p value for each test (* = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$; **** = $p \leq 0.0001$; ***** = $p \leq 0.00001$). NS (not significant) is used to denote results that are not statistically significant. NA (not applicable) is used to denote comparisons that could not be assessed due to limited sample size.

Variable	Overall	Southern sites	Northern sites
Ext enc	$Z_{2804, 408} = -7.18$ *****	$Z_{1407, 233} = -8.18$ *****	$Z_{1397, 175} = -0.43$ NS
Int enc	$Z_{1547, 107} = -6.59$ *****	$Z_{890, 41} = -8.08$ *****	NA
Disart	$Z_{2804, 193} = 1.42$ NS	$Z_{1407, 183} = 1.66$ NS	$Z_{1397, 10} = 0.24$ NS
Perio	$Z_{2792, 348} = 4.87$ ****	$Z_{1395, 173} = 17.71$ *****	$Z_{1397, 175} = -9.61$ *****
Ext bioero	$Z_{2798, 408} = 0.02$ NS	$Z_{1401, 233} = -0.01$ NS	$Z_{1397, 175} = 0.35$ NS
Int bioero	$Z_{1550, 105} = 0.37$ NS	$Z_{892, 39} = 0.3$ NS	NA
Ext FSA	$Z_{2798, 408} = 4.41$ ****	$Z_{1401, 233} = 7.2$ *****	$Z_{1397, 175} = -0.52$ NS
Int FSA	$Z_{1551, 99} = 8.53$ *****	$Z_{891, 40} = 2.47$ **	$Z_{660, 59} = 9.12$ *****
Frag	$Z_{2798, 408} = -5.84$ *****	$Z_{1401, 233} = -11.04$ *****	$Z_{1397, 175} = 2.41$ NS
Edge mod	$Z_{2798, 382} = -1.09$ NS	$Z_{1401, 233} = -3.17$ *	$Z_{1397, 149} = 2.44$ NS

and internal FSA (Table 3, Fig. 3). The results for internal damage (i.e., encrustation, bioerosion, and FSA) mirror those for external damage (Table 3). Restricting these analyses to specimens from larger sieve fractions does not affect the results.

Shell Mineralogy.—Mann-Whitney U tests applied to the pooled data (overall analysis) record significant differences between calcitic and non-calcitic specimens for encrustation (both external and internal), periostracum loss, external FSA, fragmentation, and edge modification, after Bonferroni correction (Table 4). Calcitic specimens display significantly higher levels of damage for external encrustation, internal encrustation, fragmentation, and edge modification, while noncalcitic specimens display significantly higher levels of damage for periostracum loss and external FSA (Table 4, Fig. 4). When these analyses were limited to large sieve size data, the results remained the same.

Shell Organic Content.—Combining data from all specimens across all sites (overall analysis) yielded significant differences between specimens

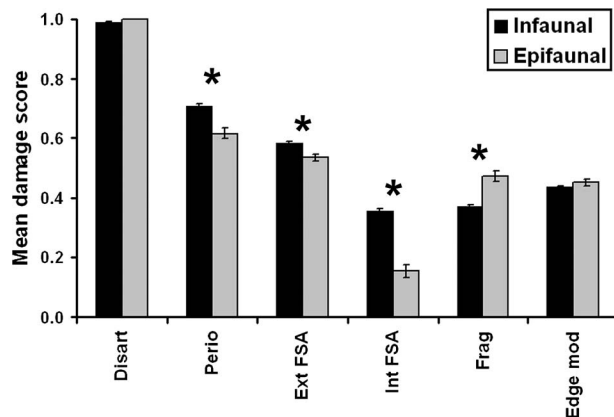


FIGURE 3—Bar graph illustrating the mean (\pm SE) damage score for epifaunal versus infaunal specimens (compiled across all samples and sites, overall analysis) for a subset of the damage variables scored. Abbreviations for damage scores as in Table 2. In the overall analysis, epifaunal specimens have significantly higher damage scores for fragmentation, while infaunal specimens have significantly higher damage scores for periostracum loss, external FSA, and internal FSA. Asterisks denote statistically significant differences.

with low versus high shell organic content for external and internal encrustation, disarticulation, external FSA, fragmentation, and edge modification, after Bonferroni correction of Mann-Whitney U tests (Table 5). Specimens with high shell organic content display significantly higher levels of damage for external and internal encrustation, disarticulation, fragmentation, and edge modification, while specimens with low shell organic content display significantly higher levels of damage for external FSA (Table 5, Fig. 5). Restricting these analyses to larger sieve fractions resulted in statistically significantly higher levels of periostracum loss in specimens with high shell organic content (Mann-Whitney U test, $Z_{1079, 177} = -2.88$; $p = 0.04$).

Effects of Intrinsic Factors: Controlling for Habitat Type

To control for extrinsic factors, the above analyses were performed separately on each of the two habitat types (southern versus northern) sampled in this study. As described above, Sites 3 and 4 (southern) represent a slightly shallower habitat with a coarser grained substrate and less variable salinity than Sites 1 and 2 (northern). For the sake of simplicity, these two habitat types are referred to as northern versus southern as opposed to deeper- and finer-grained sediment versus shallower- and coarser-grained sediment. Sampling of the southern sites produced more material than sampling of the northern sites; therefore, the results for the overall analysis consistently match those of the southern site analysis (Tables 3, 4, and 5).

Life Habit.—The only difference between the results obtained for the overall analysis and those obtained for the southern sites involves edge modification, which is significantly more severe in epifaunal relative to infaunal specimens at the latter. The northern sites recorded substantially fewer differences between infaunal and epifaunal levels of damage (Table 3). While the difference for internal FSA remained significant, the differences for external encrustation, external FSA, and fragmentation did not. Although both habitat types document a statistically significant difference between epifaunal and infaunal levels of periostracum loss, infaunal damage is greater in the southern sites and lower in the northern sites. The absence of internally encrusted or bioeroded specimens in the northern sites make it impossible to test for differences in these two damage variables while controlling for habitat type. The only statistically significant difference between infaunal and epifaunal damage that is

TABLE 4—Differences in mean damage score between calcitic and non-calcitic specimens for the overall analysis and for each habitat type analysis. Differences are assessed using Mann-Whitney *U* tests and results (after Bonferroni adjustment) are provided. Damage score abbreviations follow Table 2. Positive *Z* values denote greater damage in noncalcitic relative to calcitic specimens. Negative *Z* values denote greater damage in calcitic relative to noncalcitic specimens. The number of asterisks denotes the *p* value for each test (* = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$; **** = $p \leq 0.0001$; ***** = $p \leq 0.00001$). NS (not significant) is used to denote results that are not statistically significant. NA (not applicable) is used to denote comparisons that could not be assessed due to limited sample size.

Variable	Overall	Southern sites	Northern sites
Ext enc	$Z_{3019, 190} = -11.32$ *****	$Z_{1457, 183} = -9.39$ *****	$Z_{1562, 7} = -5.98$ *****
Int enc	$Z_{1617, 36} = -11.62$ *****	$Z_{900, 31} = -9.34$ *****	NA
Disart	$Z_{2804, 190} = 1.41$ NS	$Z_{1407, 183} = 1.66$ NS	$Z_{1397, 7} = 0.21$ NS
Perio	$Z_{2964, 173} = 12.31$ *****	$Z_{1402, 166} = 18.3$ *****	$Z_{1562, 7} = 1.52$ NS
Ext bioero	$Z_{3013, 190} = -0.79$ NS	$Z_{1451, 183} = -0.26$ NS	$Z_{1562, 7} = 0.07$ NS
Int bioero	$Z_{1620, 34} = 0.20$ NS	$Z_{902, 29} = 0.25$ NS	NA
Ext FSA	$Z_{3013, 190} = 5.89$ *****	$Z_{1451, 183} = 8.51$ *****	$Z_{1562, 7} = 2.55$ NS
Int FSA	$Z_{1614, 35} = 1.63$ NS	$Z_{901, 30} = 3.46$ **	$Z_{713, 5} = 0.29$ NS
Frag	$Z_{3013, 190} = -12.63$ *****	$Z_{1451, 183} = -13.63$ *****	$Z_{1562, 7} = -2.13$ NS
Edge mod	$Z_{2987, 190} = -7.05$ *****	$Z_{1451, 183} = -6.02$ *****	$Z_{1536, 7} = -1.70$ NS

recorded consistently across both habitat types is the higher level of internal FSA documented in infaunal versus epifaunal specimens.

Shell Mineralogy.—As expected, the southern sites generated results similar to the overall analysis (Table 4), the only difference being significantly greater internal FSA in noncalcitic specimens in the southern sites. The northern sites recorded weak, generally nonsignificant differences between noncalcitic and calcitic specimens (Table 4), with the exception of external encrustation. Calcitic specimens consistently exhibit significantly higher levels of external encrustation than noncalcitic ones across both habitat types.

Shell Organic Content.—On the whole, the southern sites produced patterns similar to the overall analysis; the patterns were in the same direction although the statistical significance varied. In the southern sites, differences in disarticulation are not statistically significant, and specimens with low shell organic display significantly higher levels of perio-

stracum loss than specimens with high shell organic content (Table 5). The differential disarticulation of specimens with high shell organic content recorded in the overall analysis is driven by specimens from the northern sites. Interestingly, the patterns for periostracum loss and external FSA in the southern sites, in which low show significantly greater damage than high, are completely opposite those recorded in the northern sites. The only significant differences documented consistently across both habitat types are fragmentation and edge modification, which are significantly more severe for specimens with high shell organic content.

Shell-damage patterns for specimens with noncalcitic shell mineralogy (Fig. 4), those with low shell organic content (Fig. 5), and those with infaunal life habits (Fig. 3) mimic each other primarily because the vast majority of infaunal taxa in the Chesapeake Bay are characterized by noncalcitic shell mineralogy (100%) and low shell organic content (75%).

DISCUSSION

Shell Damage

This survey of molluscan shell damage in the upper Chesapeake Bay identified disarticulation, external FSA, periostracum loss, edge modification, internal FSA, and fragmentation as the most common and severe forms of damage. These results agree well with Kidwell and Bosence's (1991) review of shell damage and its distribution across estuarine environments. They noted that, in these settings, dissolution is common, while bioerosion, abrasion, and fragmentation are often present. Kidwell and Bosence (1991) mentioned that specimens can also be found articulated and *in situ* in these environments, although it is rare in the upper bay.

The salinity fluctuations, shape, and latitude of the Chesapeake Bay make it difficult to identify an appropriate analogue for comparison of shell-damage profiles; few studies have examined taphonomic signatures in estuarine or marginal marine environments. For those studies that have, damage levels are generally comparable to those levels documented in this study. For example, the disarticulation levels documented in the Chesapeake Bay are extremely high (99%), but they correspond closely with the results obtained for Henderson and Frey (1986) for the northern flank of Doboy Sound (85–100%) near Sapelo Island, Georgia. FSA is considerably more common in the upper bay (external 94%, internal 79%)

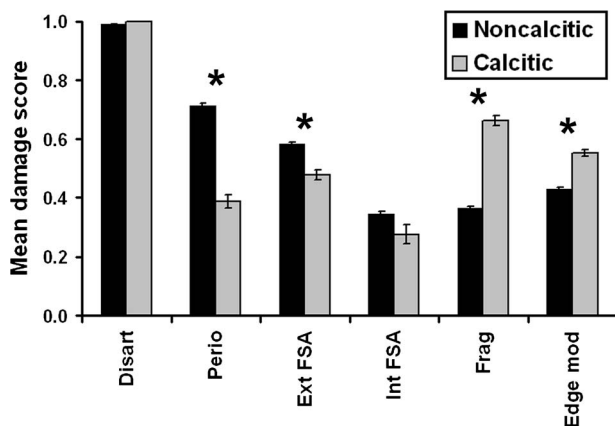


FIGURE 4—Bar graph illustrating the mean (\pm SE) damage score for specimens in different shell mineralogical categories (compiled across all samples and sites, overall analysis) for a subset of the damage variables scored. Abbreviations for damage scores as in Table 2. Asterisks denote statistically significant differences. In the overall analysis, calcitic specimens show significantly more severe damage due to fragmentation and edge modification than noncalcitic specimens, while the reverse is true for periostracum loss and external FSA.

TABLE 5—Differences in mean damage score between low and high shell organic content specimens for the overall analysis and for each habitat type analysis. Differences are assessed using Mann-Whitney *U* tests, and results (after Bonferroni adjustment) are provided. Damage score abbreviations follow Table 2. Positive *Z* values denote greater damage in low-relative to high-shell-organic-content specimens. Negative *Z* values denote greater damage in high relative to low shell organic content specimens. The number of asterisks denotes the *p* value for each test (* = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$; **** = $p \leq 0.0001$; ***** = $p \leq 0.00001$). NS (not significant) is used to denote results that are not statistically significant. NA (not applicable) is used to denote comparisons that could not be assessed due to limited sample size.

Variable	Overall	Southern sites	Northern sites
Ext enc	$Z_{2645, 345} = -7.64$ *****	$Z_{1382, 201} = -8.72$ *****	$Z_{1263, 144} = -0.52$ NS
Int enc	$Z_{1530, 51} = -9.49$ *****	$Z_{891, 26} = -10.15$ *****	NA
Disart	$Z_{2645, 345} = -5.05$ *****	$Z_{1382, 201} = -2.20$ NS	$Z_{1263, 144} = -6.06$ *****
Perio	$Z_{2620, 341} = 1.92$ NS	$Z_{1357, 197} = 16.16$ *****	$Z_{1263, 144} = -12.87$ *****
Ext bioero	$Z_{2643, 341} = -0.10$ NS	$Z_{1380, 197} = -0.148$ NS	$Z_{1263, 144} = 0.34$ NS
Int bioero	$Z_{1533, 49} = 0.25$ NS	$Z_{893, 24} = 0.23$ NS	NA
Ext FSA	$Z_{2643, 341} = 3.04$ *	$Z_{1380, 197} = 7.51$ *****	$Z_{1263, 144} = -3.21$ *
Int FSA	$Z_{1535, 49} = 1.27$ NS	$Z_{893, 24} = 2.49$ NS	$Z_{642, 25} = -1.98$ NS
Frag	$Z_{2643, 341} = -16.55$ *****	$Z_{1380, 197} = -14.61$ *****	$Z_{1263, 144} = -9.13$ *****
Edge mod	$Z_{2643, 341} = -6.29$ *****	$Z_{1380, 197} = -5.19$ *****	$Z_{1263, 144} = -3.51$ **

than in Doby Sound (defined as loss of color, gloss, periostracum, or ligament in “old” shells, 12%) or in San Luis Pass, a tidal inlet near Galveston Island (defined as abrasion, 63%, and dissolution, 28%; Davies et al., 1989). The increased levels of FSA recorded in the bay could be a result of the slightly acidic nature of the bay’s brackish water, which would be expected to etch and leach carbonate shells (Alexandersson, 1972; Pip, 1988).

Levels of fragmentation documented in the upper bay (67%) are very similar to those observed by Davies et al. (1989) in San Luis inlet (68%). Bay levels of encrustation and bioerosion (external encrustation 0.53%, internal encrustation 0.2%, external bioerosion 3.4%, internal bioerosion 0.4%) are also a close match with San Luis inlet levels for bivalves (defined as epibionts, borings, and traces, 2%) but not gastropods (44%; Davies et al., 1989). The lower level of damage observed for gastropods in the Chesapeake Bay (effectively 0%) is a pattern that Best and Kidwell

(2000a) attributed in their Panama study to limited exposure of shells above the sediment-water interface. In the present study, the sieve size used also plays a role, because smaller specimens and finer sieve sizes tend to show significantly lower frequencies of boring and encrustation (Kidwell et al., 2001; Kowalewski and Hoffmeister, 2003; Rodland et al., 2004). The substantial salinity variation in the bay is also likely to be a factor, inasmuch as many of the taxa responsible for such damage vary in abundance in response to salinity gradients (e.g., Buatois et al., 2005).

Internal damage is generally assumed to be postmortem in origin (but see Lazo, 2004), while epifaunal damage can accrue both pre- and post-mortem, leading some past workers to advocate the use of internal damage as an unambiguous measure of postmortem damage in taphofacies studies (Best and Kidwell, 2000a, 2000b). The present study is one of a number of studies to assess both external and internal measures of shell damage (Davies et al., 1989; Staff and Powell, 1990b; Callender and Powell, 1992; Callender et al., 1992; Kowalewski et al., 1994; Kowalewski et al., 1995; Kidwell et al., 2001). The majority of these studies have documented equivalent or greater damage on external surfaces for encrustation (Kidwell et al., 2001), bioerosion (Kidwell et al., 2001), and FSA (Davies et al., 1989; Staff and Powell, 1990b; Callender et al., 1992; Kowalewski et al., 1995; Kidwell et al., 2001), similar to the results reported here. The results for the upper Chesapeake Bay also indicate that, with the exception of bioerosion, internal scoring was significantly correlated with external scoring in the upper bay. This suggests that, for environments similar to those sampled here, external damage may provide a useful proxy for internal damage.

Does Shell Damage Vary According to Life Habit?

Comparisons of epifaunal versus infaunal levels of shell damage in the upper Chesapeake Bay yielded one consistent difference that was statistically significant across both habitat types. Infaunal specimens exhibit more severe internal FSA than epifaunal ones. If external damage represents both pre- and postmortem processes, while internal damage is limited to postmortem processes (but see Lazo, 2004), it follows that epifaunal taxa should show more severe external damage than infaunal. While this is the case for encrustation, fragmentation, and edge modification in the southern sites in the bay, it does not hold true across all damage variables or across all habitat types.

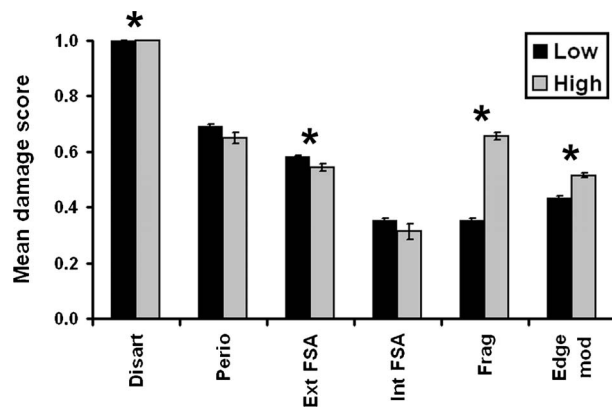


FIGURE 5—Bar graph illustrating the mean (\pm SE) damage score for specimens in different shell organic categories (compiled across all samples and sites, overall analysis) for a subset of the damage variables scored. Abbreviations for damage scores as in Table 2. Asterisks denote statistically significant differences. In the overall analysis, damage due to disarticulation, fragmentation, and edge modification is significantly more severe for specimens with high shell organic content. Specimens with low shell organic content record significantly more severe damage due to external FSA.

The majority of taphonomic studies that have compared shell damage in epifaunal versus infaunal specimens have documented higher damage levels in the former (Callender et al., 1990; Parsons and Brett, 1991; Parsons, 1993; Dent, 1995; Aguirre and Farinati, 1999; Best and Kidwell, 2000b; Kidwell et al., 2001; Lazo, 2004; Nielsen, 2004). It is worth noting that many of these studies (e.g., Parsons and Brett, 1991; Parsons, 1993; Dent, 1995) have focused predominantly on hardground as opposed to the exclusively soft-sediment environments sampled here. When Best and Kidwell (2000b) compared epifaunal versus infaunal damage in soft-substrate environments in Panama, they recorded no significant difference between the two. Similarly, the analyses of Kidwell et al. (figure 9 in 2001) of inlet floor muds in Panama showed no significant difference in shell damage due to bivalve life habit. Figure 9 of Kidwell et al. (2001) demonstrates that differences between epifaunal and infaunal shell damage vary according to environment and are rarely statistically significant.

Few studies have attempted to control for habitat while assessing the effect of life habit on shell damage. Aguirre and Farinati (1999) demonstrate that infaunal bivalve species from the late Quaternary of Argentina are better preserved than epifaunal taxa, but they also note that the former inhabit soft bottom environments whereas the latter inhabit hard-bottom environments. Since coarser-grain-size environments are often characterized by higher levels of shell damage (e.g., Best and Kidwell, 2000a), it is difficult to determine whether the differences in shell damage documented by Aguirre and Farinati (1999) are due to differences in life habit or in environment. More recently, Lazo (2004) documented a higher proportion of discoloration, corrosion (internal and external), internal encrustation, and bioerosion in epifaunal relative to infaunal specimens of *Protothaca staminea* from San Juan Island, Washington. This study is similarly complicated by the fact that infaunal *Protothaca* are limited to mud and muddy sand habitats while epifaunal *Protothaca* are restricted to gravels.

The majority of past studies have also focused on external as opposed to internal damage, with the exception of Best and Kidwell (2000b), Kidwell et al. (2001), and Lazo (2004). In the upper Chesapeake Bay, infaunal specimens exhibit significantly higher levels of internal FSA than epifaunal specimens. Best and Kidwell (2000b) also found that, although the difference was not statistically significant, infaunal taxa tended to have more severe internal FSA in muddy environments in siliciclastic regimes in Panama.

Returning to the results for the upper Chesapeake Bay, it is interesting to compare the direction of differential damage according to life habit. In the southern sites, four damage variables show greater damage in epifaunal specimens while three show the opposite (Table 3). In the northern sites, one damage variable records preferential damage in one direction, while another records it in the opposite direction. These patterns seem to suggest that taphonomic bias in one direction (e.g., epifaunal more damaged than infaunal specimens), which could lead to the selective removal of specimens with that particular life habit, would be effectively canceled out by bias in the opposite direction. This assumes, of course, that all damage variables are equally likely to lead to taphonomic bias, an assumption that has yet to be tested in the Chesapeake Bay or other estuarine environments.

The results for the Chesapeake Bay, when considered with past studies, suggest that differential damage according to life habit (either the direction or statistical significance) varies drastically according to the damage variable and the habitat type examined. Contrary to expectations, epifaunal specimens rarely show higher levels of external or internal damage than infauna in soft-sediment environments. In the upper bay, differential damage of a particular life habit is unlikely to lead to a strong taphonomic bias in either direction.

Does Shell Damage Vary According to Shell Composition?

Comparisons of shell damage in calcitic versus noncalcitic specimens in the upper Chesapeake Bay yielded a single consistent statistical dif-

ference, when the results were controlled for habitat type. Calcitic specimens, all of which are epifaunal, experience higher levels of external encrustation. Statistically significant differences between specimens with low versus high shell organic content were documented consistently for two damage variables across both habitat types. Specimens with high shell organic content record significantly greater damage due to fragmentation and edge modification than specimens with low shell organic content.

Few studies have explicitly assessed whether shell damage differs according to shell composition. Best and Kidwell (2000b) divided modern Panamanian bivalves into three categories on the basis of shell composition: (1) calcitic: equivalent to combining the calcitic and low-shell-organic-content categories in this study, (2) porcellaneous aragonitic: equivalent to combining the noncalcitic and low-shell-organic-content categories, and (3) high organic: equivalent to the high-shell-organic-content category. Best and Kidwell (2000b) found no significant differences in damage frequencies for calcitic versus porcellaneous aragonitic shells in soft-sediment environments. When the calcitic and low-shell-organic-content specimens from the upper Chesapeake Bay were compared to the noncalcitic and high-shell-organic-content specimens in the current study, Mann-Whitney *U* tests revealed only one significant difference after Bonferroni adjustment. Calcitic low-shell-organic-content specimens exhibited significantly more damage due to edge modification than noncalcitic low-shell-organic-content specimens ($Z_{2626, 17} = -4.61$, $p = 0.004$ after Bonferroni adjustment).

The dearth of a strong and consistent link between shell damage and mineralogy across both habitat types sampled in this study is perhaps not surprising. A general link between shell mineralogy and preservation in mollusks has been postulated for decades, but it is surprisingly difficult to document in the fossil record or via experimental approaches. One commonly quoted statistic contends that 94% of partially and fully calcitic living molluscan genera are recorded from the fossil record, compared with only 82% of fully aragonitic living genera (Harper, 1998b). Recent reanalysis of these same data at the family level suggests that entirely aragonitic heteroconch bivalves actually have a more complete record than calcite-bearing pteriomorphs (Harper, 1998b; see supplementary online material in Kidwell, 2005). An analysis of shell-bed thickness throughout the Phanerozoic revealed that shell mineralogy appears to exert little influence over shell-bed thickness (Kidwell and Brechley, 1996). Similarly, a comparison of genus duration in fossil marine bivalves and shell composition, including mineralogy and shell organic content, shows little relationship between the two (Kidwell, 2005).

Experimental approaches have suggested that aragonite has a lower thermodynamic stability than calcite in seawater (Morse et al., 1980; Mucci, 1983; Sanders, 2003). Unfortunately, even this basic observation breaks down with variation in ambient seawater chemistry and microstructural surface area (Flessa and Brown, 1983; Walter and Morse, 1984; Walter, 1985; Walter and Morse, 1985). Crystallite size, magnesium content of calcites, microbial activity, periostracal coverings, and organic matrix also play complex roles in the determination of shell dissolution rates (Walter and Morse, 1984; Heinrich and Wefer, 1986; Morse, 1986; Bischoff et al., 1987; Hunter, 1990; Simon and Poulicek, 1990; Glover and Kidwell, 1993; Harper, 2000).

The higher levels of fragmentation and edge modification documented in high-shell-organic-content specimens in the upper Chesapeake Bay do complement the results that Zuschin and Stanton (2001) obtained in their experiments linking shell weight to strength. They found that, as organic-rich shells degrade through time, they become progressively weaker. Similarly, Lescinsky et al. (2002) noted high frequencies of edge chipping in specimens with high shell organic content. The only differences between specimens with low and high shell organic content recorded by Best and Kidwell (2000b) in soft-sediment environments in Panama were significantly higher levels of edge rounding and internal surface degradation in high-organic-content shells in sandy mud environments.

It is difficult to imagine how the differential damage according to shell mineralogy documented in the upper Chesapeake Bay could lead to the selective removal of specimens with either calcitic or noncalcitic mineralogy. In the southern sites, four variables show higher levels of damage in calcitic relative to noncalcitic specimens, while three variables show the opposite pattern (Table 4). In the northern sites, only one variable, external encrustation, shows higher levels of damage in calcitic specimens. Once again, any taphonomic bias established in one direction (e.g., calcitic specimens more damaged than noncalcitic) is likely to be negated by bias in the other direction. This is not necessarily the case for shell organic content (Table 5). In the northern sites, five damage variables record greater damage in high-, as opposed to low-, shell-organic-content specimens. In the southern sites, four variables show greater damage in specimens with high versus low shell organic content, while two show the opposite. In this analysis, damage of high-shell-organic-content specimens far outweighs damage of low-shell-organic-content specimens, at least in northern sites. This suggests that a taphonomic filter, based on shell organic content, may exist in the upper Chesapeake Bay. It would be interesting to explore to what extent different types and levels of damage lead to taphonomic bias in these soft-sediment estuarine environments.

All in all, the results documented here and summarized from past work indicate that differential damage (the direction or statistical significance) according to shell mineralogy can vary greatly according habitat type and the damage variable scored. There is little evidence to support the preferential damage of or taphonomic bias against aragonitic specimens, at least in soft-sediment environments. The results for shell organic content are equally variable, although some evidence does suggest that specimens with high shell organic content are more prone to fragmentation and breakage. In the northern sites of the upper Chesapeake Bay, the greater levels of damage documented in high-shell-organic-content specimens may lead to selective removal of these taxa from these sites.

CONCLUSIONS

A survey of signatures of taphonomic damage in the upper Chesapeake Bay revealed that the most severe forms of shell damage are disarticulation, periostracum loss, external FSA, edge modification, fragmentation, and internal FSA. Encrustation and bioerosion are exceedingly rare in these assemblages. Internal and external surface measures of damage are statistically significantly correlated for encrustation and FSA, suggesting that, in these particular environments, external measures may provide a useful proxy for internal ones.

Shell damage differs according to both life habit and shell composition, but the significance and direction of differential damage tends to vary according to the type of damage assessed or the habitat type sampled. For example, periostracum loss is significantly greater in infaunal specimens and specimens with low shell organic content in the southern sites and significantly lower in the northern sites. Similarly, external FSA is significantly lower in specimens with low shell-organic content in the northern sites and significantly greater in the southern sites. The only patterns of differential damage that consistently were statistically significant across both habitat types were internal FSA, external encrustation, and fragmentation and edge modification. Contrary to expectations, infaunal specimens exhibit significantly higher levels of internal FSA than epifaunal specimens. Along the same lines, calcitic specimens show greater external encrustation than noncalcitic specimens. High-shell-organic-content specimens exhibit significantly greater fragmentation and edge rounding than low-shell-organic-content specimens, regardless of habitat type. The only pattern of differential damage that might lead to a taphonomic filter in the upper Chesapeake Bay is the preferential damage of high-shell-organic-content specimens in the northern sites.

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