PALAIOS
Emphasizing the impact of life on
Earth's history

PALAIOS, 2006, v. 21, p. 442–450
Research Article
DOI: 10.2110/palo.2005.P05-083R

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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

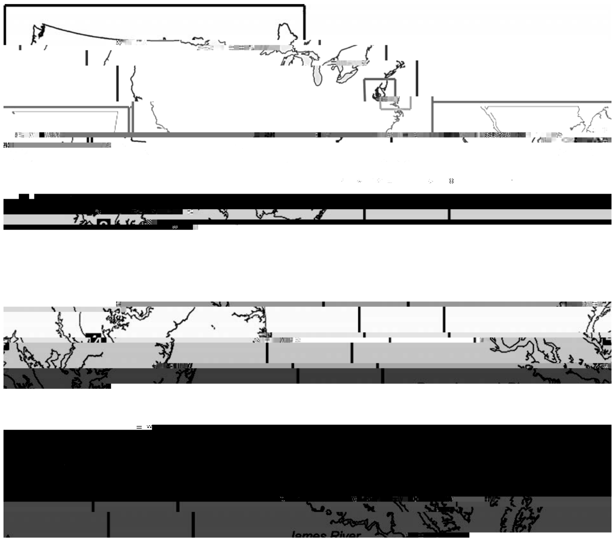

FIGURE 1—Map of the Chesapeake Bay (Atlantic coast, North America) illustrating the sites sampled in this study.

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;

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 tests and results (after Bonferroni adjustment) are provided. Abbreviations for damage scores as in Table 2. Positive values denote greater damage in infaunal relative to epifaunal specimens. Negative values denote greater damage in epifaunal relative to infaunal specimens. The number of asterisks denotes the value for each test (* = ≤ 0.05; ** = ≤ 0.01; *** = ≤ 0.001; **** = ≤ 0.0001; ***** = ≤ 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.

.—Mann-Whitney tests applied to the pooled data (overall analysis) record significant differences between calcitic and noncalcitic 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.

.—Combining data from all specimens across all sites (overall analysis) yielded significant differences between specimens 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 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 test, $_{1079, 177} = -2.88$; $= 0.04$).

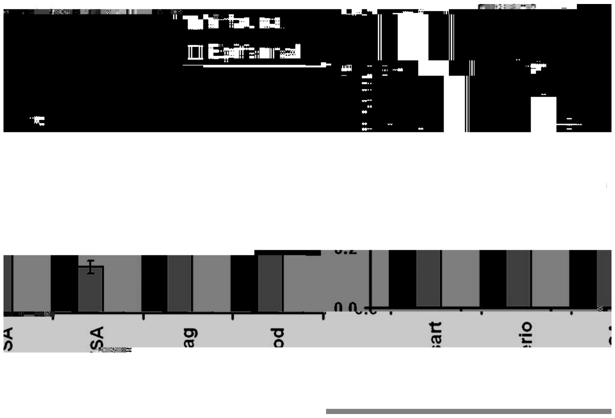

FIGURE 3—Bar graph illustrating the mean (±SE) damage score for epifaunal versus infaunal specimens (compiled across all samples and sites, overall analysis) for a subset of the damage variables scored. Abbreviations for damage scores as in Table 2. In the overall analysis, epifaunal specimens have significantly 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.

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).

.—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 tests and results (after Bonferroni adjustment) are provided. Damage score abbreviations follow Table 2. Positive values denote greater damage in noncalcitic relative to calcitic specimens. Negative values denote greater damage in calcitic relative to noncalcitic specimens. The number of asterisks denotes the value for each test (* = ≤ 0.05; ** = ≤ 0.01; *** = ≤ 0.001; **** = ≤ 0.0001; ***** = ≤ 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

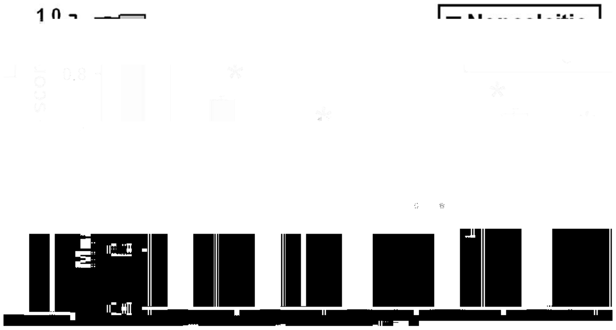

FIGURE 4—Bar graph illustrating the mean (illustratingm00(1d/ore3cph)-3u]TJ80014.3Tm0OB0154hfif7008498.6499Tm0498.6499iled***183Bar1dcr9w1fi29(Feh2t3F41T5330.5f79107.429031c

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 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, corrasion (internal and external), internal encrustation, and bioerosion in epifaunal relative to infaunal specimens of from San Juan Island, Washington. This study is similarly complicated by the fact that infaunal are limited to mud and muddy sand habitats while epifaunal 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 see(another)-313gimes in an-wellhav73.5(anchgge-319.uhonom(rehgge-31biaalso)-319oppos325.3(nfo

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