

Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. II. Effect of bivalve life habits and shell types

Mairi M. R. Best and Susan M. Kidwell

Abstract.—Bivalve death assemblages from subtidal environments within the tropical Bocas del Toro embayment of Caribbean Panama permit a test of the extent to which levels of damage are determined by the intrinsic nature of shell supply (proportion of epifaunal species, thick shells, calcitic shells, low-organic microstructures), as opposed to the extrinsic postmortem environment that shells experience. Only damage to interior surfaces of shells was used, to ensure that damage was unambiguously postmortem in origin. We find that facies-level differences in patterns of damage (the rank order importance of postmortem encrustation, boring, edge-rounding, fine-scale surface degradation) are overwhelmingly controlled by environmental conditions: in each environment, all subsets of the death assemblage present the same damage profile. The composition of shell supply affects only the intensity of the taphonomic signature (i.e., percentage of shells affected), and only in environments containing hard substrata (patch reefs, *Halimeda* gravelly sand, mud among patch reefs). In these environments, epifauna, whether aragonitic or calcitic and whether thin or thick, exhibit significantly higher damage than co-occurring infauna, probably due to the initial period of seafloor exposure they typically experience after death. Thick shells (>0.5 mm), regardless of life habit or mineralogy, are damaged more frequently than thin shells, probably because of selective colonization by fouling organisms. Calcitic shells show no consistently greater frequency of damage than aragonitic shells, and high-organic microstructures yield mixed patterns. Taphofacies surveys in such depositional systems could thus be confidently based on any subset of the fauna, including diagenetically residual assemblages of calcitic shells and thick-shelled molds. Further tests are needed to determine whether the higher levels of damage observed on some subsets of shells are a consequence of greater time-averaging (thus lower temporal resolution), greater exposure time, preferential attack (potential bias in relative abundance), or some combination of these. Paleobiologically, however, the implication is that ecological subsets of bivalve assemblages are not isotaphonomic, either in tangible damage or in probable bias, within hard-substrate environments, although they may be within soft-sediment environments. In actualistic studies, targeting broad classes of taxa for comparison across environments maximizes our ability to extrapolate taphonomic guidelines into the fossil record, where life habits, skeletal types, and shallow subtidal habitats have dramatically different patterns of abundance and deployment.

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Introduction

Paleontologists have long recognized that the quality of fossil preservation varies among environments (see historical review by Cadée [1991]). The classic actualistic work on this phenomenon was by Schäfer (1972), who differentiated a series of idealized biofacies on the basis of death assemblage characteristics (are taxa largely indigenous or exotic to the facies? disturbed from life positions? damaged by postmortem processes?). “Taphofacies analysis” (Speyer and Brett 1986) has increasingly focused on the quantitative damage profile or “taphonomic signature” of death assemblages (e.g., observed frequency of bored and encrusted hard parts, extent of skeletal

disarticulation and fragmentation), with the aim of developing a set of criteria for paleoenvironmental interpretation and for recognizing between-habitat transport of shells (e.g., Davies et al. 1989; Staff and Powell 1990; Anderson and McBride 1996; Brachert et al. 1998).

One aspect of marine taphofacies that has remained unclear is the extent to which facies-level differences in the quality of preservation are due to differences in postmortem conditions as opposed to differences in the material supplied by living organisms. That is, what is the relative importance of the *extrinsic* environment of accumulation (destructive physical, chemical, and biological agents, scales of time-averaging), as opposed to the *intrinsic* attri-

butes of tissues produced or otherwise introduced to that environment (e.g., types of hard-part construction, condition upon death)? Determining the relative contributions of these factors would permit a better evaluation of (1) the limits of extrapolation back into the fossil record, where the composition of skeletal supply differs owing to evolution (e.g., different proportions of epifauna and infauna in soft substrata, of thick versus thin shells, of shell mineralogies and microstructures), and (2) the relative tendencies of different classes of skeletal supply to accrue postmortem damage, and thus how best to target field effort when conducting taphofacies analysis for paleoenvironmental differentiation. The results also bear on the question of (3) differential bias (underrepresentation) of taxa, and particularly of entire subsets of faunas, in death assemblages. Although direct experimentation is necessary to establish causation, strong links between intrinsic attributes and particular levels or patterns of damage indicate the potential for bias in preservation.

Taphofacies analyses have tended to focus on the role of extrinsic postmortem conditions in generating damage profiles, but most workers clearly appreciate that both intrinsic and extrinsic factors (nature and nurture) are important (Meyer et al. 1989). However, distinguishing these effects can be difficult. Nebelsick (1992), for example, attributed much of the variation in damage profiles of echinoid death assemblages in Safaga Bay, northern Red Sea, to the ecological dominance of thin-shelled regular echinoids in hardground habitats and of robust clypeasteroids in sands, but the spatial segregation of taxa was too strong to differentiate taxonomic and environmental effects. Similarly, Parsons and Brett (1991) postulated that differences in shell supply probably affected taphonomic signatures in molluscan death assemblages from the northeastern Caribbean, because nonreef assemblages contained virtually none of the epifaunal taxa that carried the heaviest damage in reef assemblages. An unambiguous test was not possible, however, because an unknown portion of the damage to epifauna might have occurred during life rather than after death (taphonomic signatures were based on dam-

age to both interior and exterior surfaces of shells). Studies that have evaluated a single "target taxon," either to control for supply effects or as an exemplar of an entire class of shells, have yielded mixed results: some taxa show little environmental variation in damage (Dent 1995; Gardiner et al. 1995), other taxa are highly variable (Meldahl and Flessa 1990; Cutler 1995), and different taxa may vary in different ways across the same suite of environments (e.g., Fiege and Fürsich 1991; Dent 1995; Pandolfi and Greenstein 1997). In light of these mixed outcomes, the magnitude and nature of the effect that shell supply has on assemblage-level damage profiles deserves fuller testing.

Here, we test the effect of intrinsic biological factors on preservation in five tropical subtidal environments of the Bocas del Toro embayment in Caribbean Panama (Fig. 1). In our taphonomic survey of this area (Best and Kidwell this issue), we found that levels of damage were greater in bivalve death assemblages from environments with hard substrata than in exclusively soft-sediment environments, and that differences among environments within these sets were relatively subtle. A combination of extrinsic environmental differences probably drives this basically dichotomous pattern, including differences in rapidity and continuity of shell burial, and in the effectiveness of burial in protecting shells from various foulers and indeed in creating less tolerable conditions for foulers (linked to sediment grain size). Field experiments are being analyzed to test the roles of specific environmental conditions. However, the striking differences in death-assemblage condition between hard-substrate and soft-sediment environments may be in part a consequence of differences in shell supply, since hard-substrate assemblages contain a much larger proportion of epifaunal bivalves (average 42% versus 6% respectively; Table 3 in Best and Kidwell this issue). Epifaunal lifestyles among bivalves are stereotypically linked to calcitic shell compositions and thick shells, which in laboratory experiments are correlated with greater shell durability (e.g., Chave 1964; Flessa and Brown 1983; review by Kidwell and Bosence 1991).

Bocas death assemblages are especially advantageous for such a test:

1. Except for modest amounts of shell transported from patch reefs into immediately adjacent muds ($\leq \sim 10$ m laterally), shell supply is derived from the local benthic community (Best and Kidwell this issue); thus, facies-level differences in damage are not smeared by large quantities of exotic shells.
2. Epifaunal bivalves are reasonably abundant in death assemblages from four of the environments and infaunal bivalves are abundant in all five (Best and Kidwell this issue). Death-assemblage compositions are thus not so strongly segregated to prevent cross-environment comparisons of the effect of life habit.
3. Intrinsic attributes of interest are not overwhelmingly intercorrelated in this bivalve fauna: (a) both infauna and epifauna comprise approximately equal numbers of thin-shelled and thick-shelled taxa, and, (b) although all shells composed of foliated calcite are from taxa with epifaunal life habits, an equal number of epifaunal taxa and the majority of epifaunal individuals have shells that are entirely or partly aragonitic (Table 1).
4. Only shells >8 mm were analyzed and the vast majority fell within the 8–20 mm range. Thus, any size effects are minimized.
5. Finally, in constructing damage profiles, only damage to the interior surfaces of shells was considered, and thus all encrustation, boring, commissural edge-rounding, and fine-scale alteration of shell material are unambiguously postmortem in origin.

Study Area and Methods

Bocas del Toro is a large, geomorphically complex embayment of the Caribbean coast of Panama at 9 degrees North (Fig. 1; see Best and Kidwell this issue for more detailed description). Subtidal habitats are dominated by siliciclastic sands and muds shed from the Panama mainland and from islands within the embayment. Patch reefs rise up from these

muddy seafloors and, together with algal meadows, constitute point sources of pure carbonate sediments. Death assemblages were collected from five sedimentary environments in November 1994 (same samples and stations as Best and Kidwell this issue; stations are nonconsecutively numbered polygons in Fig. 1). Three environments include some proportion of hard substrata: (1) patch reefs (primarily hard bottom of live and dead coral and coralline algae, with pockets or veneers of shelly carbonate sand; sampled at 14–16 m depth); (2) *Halimeda*-rich gravelly sand (coralgal meadows swept by strong currents and containing trace amounts of siliciclastic sand, sampled at 12–13 m depth); and (3) siliciclastic to mixed carbonate-siliciclastic mud among closely spaced patch reefs (bioclastic grain content >2 mm varies with proximity to reefs, sampled at 14–20 m depth). The other two environments are exclusively soft-sediment habitats (sampled at 13–29 m depth): (4) siliciclastic sandy mud (from wave- and current-affected margins of Canal del Tigre) and (5) homogeneous siliciclastic clayey mud (backwaters of Bahía Azul, and extensive submarine plain of innermost Laguna de Chiriquí, which has 37 m maximum depth).

Taphonomic data were collected from bivalve shells and fragments >8 mm. Damage profiles for the entire bivalve assemblage are based on the six taphonomic variables showing greatest variation. These are (1) disarticulation (presence versus absence); (2) fragmentation (versus unbroken); and, using shell interiors only and $10\times$ magnification, (3) encrustation (presence versus absence; plus taxonomic composition of encrusters); (4) non-predatory boring (presence versus absence; plus taxonomic composition of borers); (5) rounding of commissural edges (versus pristine, chipped, or thinned); and (6) fine-scale alteration of the shell's surface texture outside the pallial line (surface chalky and pitted, or eroded, versus pristine, dulled, chalky, or pitted; SEM required to determine specific cause, e.g., dissolution of crystallites versus maceration of organic matrix versus microboring).

For this study, each bivalve specimen was also identified taxonomically and scored for intrinsic attributes: bivalve life habit (epifau-

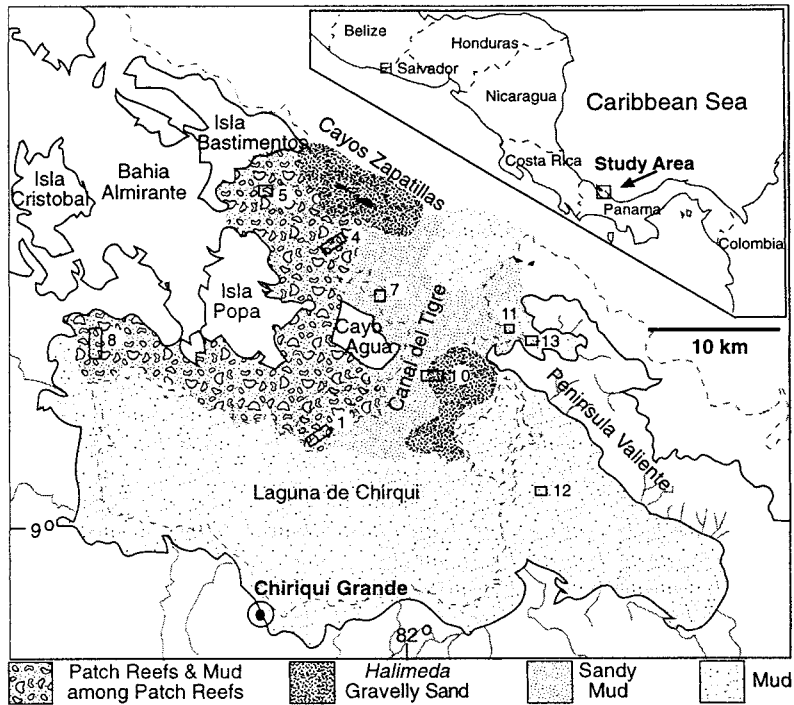


FIGURE 1. Map of sedimentary environments in Bocas del Toro study area, Caribbean Panama. Patch reefs and gravelly algal meadows provide point sources of carbonate sediment production and hard-substrate environments within a system dominated by siliciclastic mud. Subtidal areas in white are outside study, and no data are available; 20-m bathymetric contour.

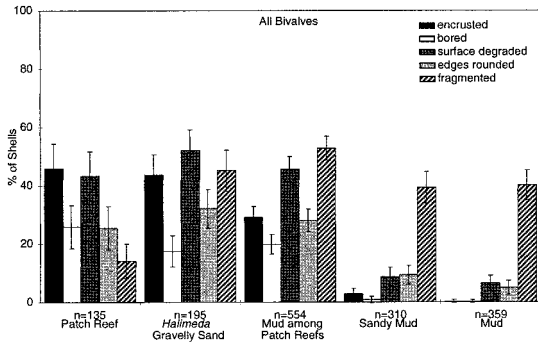


FIGURE 2. Damage profiles of total bivalve assemblages, based on pooled data from all samples in each sedimentary environment (from Best and Kidwell this issue). Only damage to shell interiors is considered. Shells in environments with hard substrata (patch reef, *Halimeda* gravelly sand, mud among patch reefs) show higher frequencies of all types of damage than shells in exclusively soft-sediment environments (sandy mud, mud). The only exception is fragmentation, which is high in all environments except patch reefs, where many bivalve shells were cemented to or wedged within reef rubble. Because fragmentation is otherwise high, regardless of environmental energy, it probably reflects predation rather than conditions of postmortem accumulation.

nal, infaunal, semi-infaunal; i.e., likely position at time of death), attachment (free-living, byssate, cemented, boring), shell thickness ($>$ or $<$ 0.5 mm), and shell mineralogy and microstructure (low-organic foliated calcite, low-organic porcellaneous aragonite, low-organic bimineralic, high-organic aragonite, and high-organic bimineralic). Information on bivalve shell compositions at the family level was derived from many sources, summarized in Kidwell and Brenchley 1996.

Character of Total Death Assemblage

Each of the five sedimentary environments in the embayment yields a distinctive damage profile (taphonomic signature; Best and Kidwell this issue) (Fig. 2). Disarticulation and fragmentation are high across all environments except patch reefs, where many specimens were found still cemented to or wedged within reef rock (rubble retrieved by dredge). Because there is no correlation between damage levels and either water depth (range 12–29 m) or inferred water energy (relatively ex-

TABLE 1. Numbers of individuals (numerator) and taxa (denominator) in intrinsic groupings of bivalves. Total numbers of taxa are corrected for species that are represented by both thin- and thick-shelled individuals.

	Epifauna			Infauna			Grand total
	Thin	Thick	Total	Thin	Thick	Total	
Foliated calcite ¹	68/15	79/12	147/21	0/0	0/0	0/0	147/21
Porcellaneous aragonite ²	10/3	204/12	214/10	602/30	435/28	1037/45	1251/55
High-organic ³	37/5	9/4	46/6	69/2	39/3	108/4	154/10
Total	115/23	292/28	407/37	671/32	474/31	1146/49	1552/86

¹ Foliated calcite = shells dominated by low-organic foliated calcite microstructure, including biminerale spondyliids, limids, plicatulids.

² Porcellaneous aragonite = shells lacking calcite and dominated by low-organic cross-lamellar and complex cross-lamellar aragonite microstructures.

³ High-organic = shells dominated by some combination of high-organic microstructures (nacreous aragonite, prismatic calcite, interleaved porcellaneous aragonite and conchiolin).

posed stations 1, 7, 10, and 11, versus lee stations 5, 8, 12, and 13, in Fig. 1) Best and Kidwell (this issue) concluded that fragmentation and disarticulation were probably biogenic rather than physical in origin. This damage may, in fact, be largely due to predation rather than to strictly postmortem processes.

The other four variables in the damage profile (encrustation, boring, edge-rounding, and fine-scale alteration) are strictly postmortem in origin because they were measured from shell interiors. Damage of these types is significantly higher in hard-substrate environments than in exclusively soft-sediment environments. Damage profiles of environments differ either (1) in the specific ranking of variables (e.g., fine-scale alteration and encrustation are tied for top rank in the patch reef profile, but are ranked 1 and 2 in both *Halimeda* gravelly sand and in mud among patch reefs) or (2) in the magnitudes of similarly ranked variables (e.g., assemblages from homogeneous muds have significantly less encrustation, boring, and edge-rounding than those from sandy muds; 95% confidence interval [CI]). Preliminary scanning electron microscopy indicates that edge-rounding and fine-scale surface alteration are caused primarily by biological attack (microbioerosion, maceration), as of course are encrustation and boring.

Experimental work by many workers, both in the lab and field (reviewed by Kidwell and Bosence 1991; Parsons and Brett 1991), as well as our ongoing experiments in Panama (Best 1998; Best and Kidwell 1996), indicate that, although microbial attack continues during burial, other kinds of damage accrue either exclusively or most rapidly during shell expo-

sure on the seafloor. Therefore, key extrinsic environmental factors differentiating taphofacies within the Bocas del Toro embayment were probably (1) the delayed burial or more frequent exhumation of shells in hard-substrate environments (i.e., greater total residence time on or just below the sediment-water interface in relatively coarse and permeable sediments) and (2) the rapid and more constant cover of shells by (siliciclastic) muds in the exclusively soft-sediment environments, which are also less favorable habitats for light-sensitive fouling taxa (Best and Kidwell this issue).

Tests of Intrinsic Factors

Effect of Life Habit.—Operationally, "epifauna" includes all taxa that live largely or entirely above the sediment-water interface. Such species cement themselves to hard substrata ("cementers"), are byssally attached to or nestle among hard substrata, live unattached upon the seafloor (free-living), bore into hard substrata, or live semi-infaunally. That is, "epifauna" includes all taxa that, upon death, would ordinarily lie on or largely above the granular sediment-water interface, accessible to overlying water and the array of taphonomic processes that operate there. "Infauna" refers only to bivalves that live fully within sediments, and thus, upon death, would ordinarily lie within the sedimentary column, requiring postmortem exhumation to be exposed to overlying water. Overall, sampled Bocas death assemblages comprise 37 epifaunal taxa and 49 infaunal taxa, totaling 407 and 1146 individuals respectively (Table 1).

Within individual samples, both cementing and noncementing epifaunal bivalves show

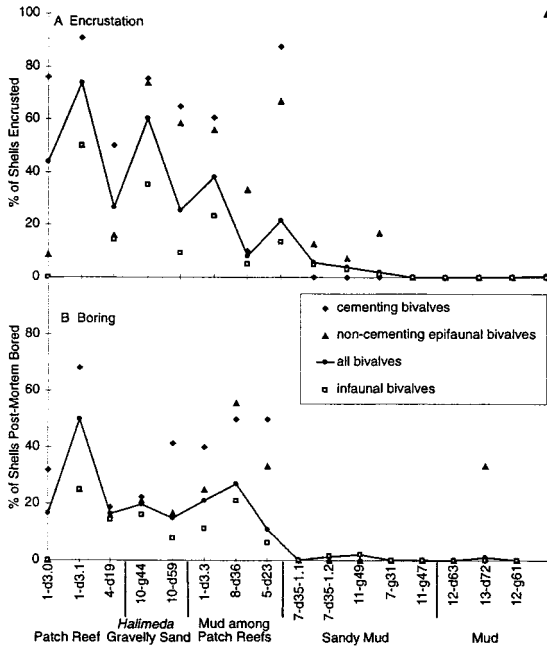


FIGURE 3. On a sample-by-sample basis, shells from epifaunal species have higher frequencies of encrustation (A) and macroscopic nonpredatory boring (B) than infaunal species. Cementing epifauna typically have higher frequencies of damage than noncementing epifauna.

higher than expected frequencies of encrustation and nonpredatory boring, given their abundance in the total death assemblage, and infauna consistently show lower than expected levels (Fig. 3).

Damage profiles of the five environments based on pooled samples are presented in Figure 4; all taphonomic variables are plotted except disarticulation, which is high in all environments. Both epifauna and infauna show the same environmental pattern that is evident in the total assemblage (Fig. 2): damage levels are significantly higher in hard-substrate environments (patch reef, *Halimeda* gravelly sand, mud among patch reefs) than in exclusively soft-sediment environments (sandy mud, mud). The most significant difference between epifaunal and infaunal shells is that, within hard-substrate environments, epifaunal shells show significantly higher frequencies of all kinds of damage (~20 percentage points higher) than infaunal shells. (The only exception is the significantly lower fragmentation of epifaunal shells in patch reefs—many of which are still

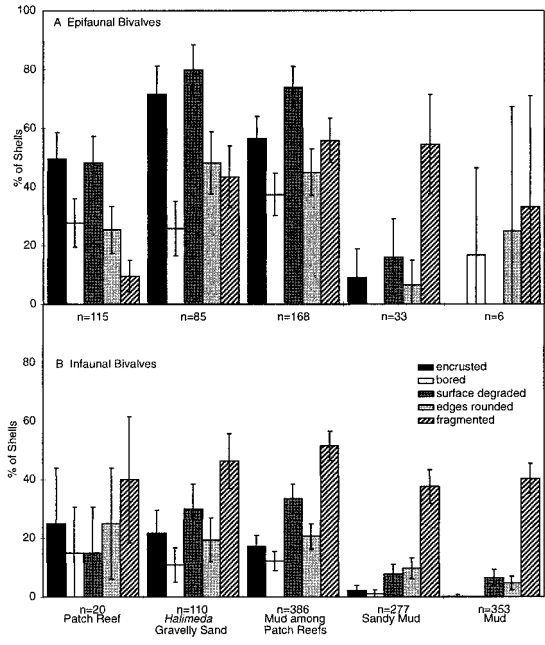


FIGURE 4. Pooled by environment, epifaunal (A) and infaunal shells (B) both show higher frequencies of post-mortem damage in hard-substrate environments than in soft-sediment environments (95% confidence intervals here and in all other figures). In the three hard-substrate environments, epifauna show higher frequencies of damage than infauna, but damage types have the same rank-order importance or nearly so. In soft-sediment environments, epifaunal profiles are not significantly different from infaunal profiles given the small numbers of epifaunal shells.

attached or wedged within the reef-rock framework—in contrast to infauna, which show high fragmentation in all environments.) Consequently, the taphonomic contrast between hard-substrate and exclusively soft-sediment environments is much greater when based on epifaunal shells than on infaunal shells (difference of ~30 percentage points versus ~10 percentage points).

Although epifauna show higher overall frequencies of damage than infauna in hard-substrate environments, the rank order of post-mortem variables—that is, the pattern of damage—is identical or nearly so (Fig. 4). In *Halimeda* gravelly sand, the rank order of variables for epifaunal shells is surface degradation (most frequent damage), encrustation, edge rounding, and boring (SD > ENC > ER > BOR), and, within the narrower range of values for infauna, SD > ENC = ER > BOR. In mud among patch reefs, the epifaunal pro-

file is $SD > ENC > ER \geq BOR$, and for infauna, $SD > ER \geq ENC > BOR$. In patch reefs, the epifaunal order is $SD = ENC > ER = BOR$, and for infauna, $SD = ENC = ER = BOR$ because of large error bars. In sandy mud and mud, epifaunal shell damage is not significantly different from zero for any variable except SD in sandy mud; among the far more numerous infaunal shells, the only non-zero variables in either environment are $SD = ER$. Given the number of comparisons, this slight variation in rank orders is expected by chance.

Thus, with the exception of fragmentation in patch reefs, epifauna show significantly higher frequencies of all types of damage than infauna in the three hard-substrate environments, but the basic taphonomic profile (ranking of types of damage) is very similar to that of infauna.

Effect of Bivalve Shell Thickness.—With the exception of fragmentation, thick shells (>0.5 mm) show significantly higher levels of damage in hard-substrate environments (patch reef, *Halimeda* gravelly sand, mud among patch reef) than in soft-sediment environments (sandy mud, mud; frequencies of ~ 30 – 70% versus $<10\%$, Fig. 5A). This is the same broad trend seen in the total death assemblage (Fig. 2). Thin shells (<0.5 mm) exhibit the same trend (Fig. 5B), but differences are muted (20 – 40% damage frequencies in hard substrata versus $\sim 10\%$ in soft-sediment) and not all pairwise comparisons are significant. For example, surface degradation is significantly higher for thin shells only in the *Halimeda* gravelly sand and in mud among patch reef environments, and edge-rounding is significantly higher only in mud among patch reefs. Both thick and thin shells show significantly lower fragmentation in patch reefs than in other environments.

Comparing thick and thin shells within each environment, the most notable difference is within hard-substrate environments, where thick shells show much higher damage frequencies than do thin shells (~ 20 percentage points higher). In detail, thin shells are significantly less fragmented than thick shells in patch reefs, and significantly more fragmented in mud among patch reefs, sandy mud, and mud. The rank ordering of taphonomic vari-

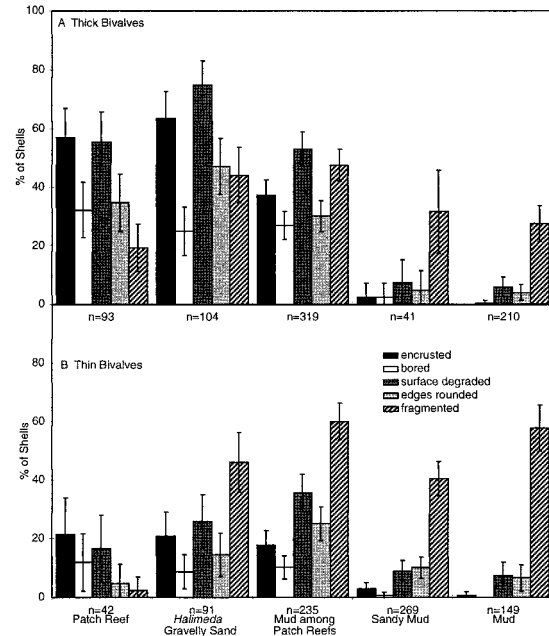


FIGURE 5. Thick shells (>0.5 mm) (A) and thin shells (B) both show higher frequencies of postmortem damage in hard-substrate environments than in soft-sediment environments. In the three hard-substrate environments, thick shells show much higher frequencies of damage than thin shells, but damage types have the same rank-order importance or nearly so. In soft-sediment environments, profiles of thick shells are not significantly different from those of thin shells.

ables in each environment is otherwise generally the same for both thick- and thin-shell data sets. In patch reef environments and *Halimeda* gravelly sand, CIs for thin shells are too large given the low frequencies to rank variables confidently, but strong similarities to the respective thick-shell rankings are evident: in patch reefs, surface degradation and encrustation are most frequent, followed by edge-rounding and boring ($SD = ENC > ER = BOR$), and in *Halimeda* gravelly sand, both thick and thin shells have profiles with $SD > ENC > ER > BOR$. In mud among patch reefs, thick- and thin-shell profiles differ in the order of only one variable, encrustation, which drops from second to third position: for thick shells, $SD > ENC > ER = BOR$, whereas for thin shells, $SD > ER > ENC > BOR$. In sandy mud, both thick- and thin-shell taxa show $SD = ER > ENC = BOR$, and in mud, both have profiles $SD = ER > ENC = BOR = 0$.

Thus, with the exception of peri-mortem

fragmentation, thick shells exhibit significantly higher frequencies of damage than thin shells in the set of hard-substrate environments, but the basic pattern of damage is otherwise extremely similar to that of thin shells in both these and soft-sediment environments.

Effect of Shell Mineralogy and Microstructure.—To test the effect of shell composition on damage profiles, we grouped taxa into three categories (Fig. 6). Operationally, “calcitic bivalves” include all shells composed of foliated calcite, which is the relatively low-organic calcitic microstructure used by pectinids, ostreids, and, in combination with low-organic porcellaneous aragonite, by limids, spondylids, and plicatulids. Because foliated calcite forms the outer shell layer in these biminerals taxa, and thus the area outside the pallial line on shell interiors, we group these biminerals taxa with entirely calcitic taxa. This calcitic category constitutes 10% of all shells (Table 1). “Porcellaneous aragonitic bivalves” include calcite-free shells dominated by low-organic aragonitic microstructures such as cross-lamellar and complex cross-lamellar, and dominate all assemblages (80% of all shells; Table 1). This includes most infaunal bivalve taxa sampled in Bocas environments, and also many epifauna, such as chamids, arcids, anadarids, barbatiids, gastrochaenids, hiattellids, and lithophagids. The third category comprises all “high-organic shells,” whose variants are unevenly distributed among environments. These include (1) entirely aragonitic pandorids composed of high-organic nacreous and homogeneous aragonites, (2) nuculanids, whose shells are interleaved mixtures of porcellaneous aragonite and conchiolin (the only high-organic taxon in sandy mud and mud environments), and (3) biminerals taxa such as isognomids and pinnids, which combine nacre and high-organic prismatic calcite (exclusively in hard-substrate environments) (sources of information on microstructure types in Kidwell and Brenchley 1996).

The basic trends of the total death assemblage are captured by both the foliated calcite and the porcellaneous aragonite subsets of taxa: both subsets show higher frequencies of damage in hard-substrate environments than

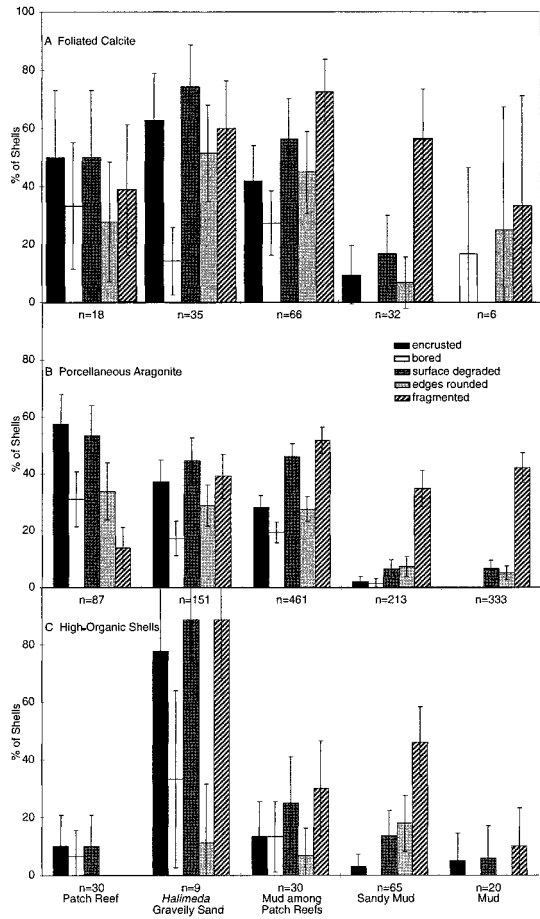


FIGURE 6. Shells that include foliated calcite (A) and aragonitic shells dominated by porcellaneous microstructures (B) both show higher frequencies of post-mortem damage in hard-substrate environments than in soft-sediment environments. In the three hard-substrate environments, damage types have the same rank-order importance or nearly so in both subsets of the bivalve death assemblage; calcitic shells have higher frequencies of most types of damage than co-occurring aragonitic shells in gravelly sands, but not in patch reefs or mud among patch reefs. High-organic shells (C), constructed of some combination of homogeneous aragonite, nacre, and prismatic calcite, have highly variable damage profiles.

in soft-sediment environments (Fig. 6A,B). Again, the only exceptional variable is fragmentation, which for porcellaneous aragonite shells is high in all environments except patch reefs. CIs for the foliated calcite data are too large to detect any trend in fragmentation. Within each soft-sediment environment, calcite and porcellaneous aragonite shells show no significant differences in frequencies of

damage (Fig. 6A,B): all types of damage other than fragmentation are low ($\leq \sim 10\%$).

Within each hard-substrate environment, pairwise comparisons of damage to calcitic and aragonitic shells mostly yield no significant or consistent differences. In patch reefs, encrustation and surface degradation are marginally lower for calcitic shells than for aragonitic shells, but in mud among patch reefs, encrustation and edge-rounding are marginally *higher*. The strongest divergence is in *Halimeda* gravelly sand, where encrustation, surface degradation and edge-rounding (but not boring) are significantly higher for calcitic shells than aragonitic shells. Despite these slight differences in frequency, the relative ranking of damage types for the two shell types does not differ significantly. In patch reefs, the ranking is ENC = SD > BOR = ER for both groups (with aragonite having marginally higher overall frequencies); in *Halimeda* gravelly sand, the ranking is SD > ENC > ER > BOR for both groups (with calcite having higher overall frequencies); and in mud among patch reefs, the ranking is SD > ER = ENC > BOR (with calcite having marginally higher overall frequencies).

Assessing the effect of organic content is less straightforward. (1) High-organic shells in sandy mud and mud (all pure-aragonite nuculanids) show no significant differences in frequency of damage compared with counterpart low-organic porcellaneous aragonitic shells in these environments (compare Fig. 6C with Fig. 6B), with the exception of significantly higher levels of edge-rounding and surface degradation among high-organic shells in sandy mud. (2) High-organic shells in patch reefs and mud among patch reefs (dominantly bimineralic forms) show lower frequencies of damage than counterpart low-organic foliated calcite shells (compare Fig. 6C with Fig. 6A), whereas there are no significant differences within *Halimeda* gravelly sand environments.

Thus, with the caveat of relatively large CIs, both low-organic foliated calcite and low-organic porcellaneous aragonite shells show greater damage in hard-substrate than in soft-sediment environments, consistent with the trend in the total bivalve death assemblage. Within environments, neither group shows a

consistently higher frequency of damage than the other does, and among hard-substrate environments the two groups exhibit identical patterns of damage (ranking of damage types). High-organic microstructures show less damage than low-organic microstructures of the same mineralogy in two of three hard-substrate environments, but greater damage than low-organic counterparts in one of the two soft-sediment environments. Thus, mineralogy and microstructure convey no consistent effect on taphonomic damage.

Discussion

Damage to shell interiors (encrustation, boring, edge-rounding, and fine-scale surface degradation) is unambiguously postmortem in origin. Patterns of damage within Bocas bivalve assemblages thus permit us to determine the roles of extrinsic and intrinsic taphonomic factors in generating facies-level differences in shell damage, and to discriminate links between postmortem damage and specific intrinsic characters (life habit, shell thickness, shell mineralogy and microstructure). As a complement to experiments that measure the reactive *rates* of shell types, our results indicate the *net product* of differential shell reactivities in a time-averaged system.

Our key findings are: (1) each subset of the bivalve fauna (four pairwise divisions: epifaunal versus infaunal life habit, thick versus thin shell, foliated calcite versus porcellaneous aragonite, and high- versus low-organic microstructures) displays greater damage in hard-substratum environments than in soft-sediment environments, as also observed in the pooled data set (Fig. 2); (2) in any given environment, all subsets exhibit the same or a nearly identical pattern of damage in terms of the rank order of taphonomic variables; and (3) subsets of shells differ in damage from one another, if at all, only in the percentage of shells affected (Table 2).

These empirical results have a series of implications, both for the behavior of taphonomic systems and for the sedimentologic and paleobiologic value of death assemblages.

Relative Importance of Extrinsic and Intrinsic Factors.—In Bocas del Toro, extrinsic environmental conditions exert an overwhelming ef-

TABLE 2. Summary of results.

Subsets of taxa compared	Does each subset differentiate hard- and soft-substrate facies?	Do frequencies of damage differ significantly between subsets?		Do rank orders of damage in subsets differ significantly?
		In hard substrata	In soft sediment	
Epifauna vs. infauna	yes	yes, epifauna > infauna	no	no
Thick- vs. thin-shelled	yes	yes, thick > thin	no	no
Calcite vs. aragonite (both low-organic)	yes	no	no	no
High- vs. low-organic	high-organic does not	low-organic > high-organic in 2 of 3 facies	high-organic > low-organic in 1 of 2 facies	no

fect on death assemblage condition: all [biological] subsets of the bivalve death assemblage of a given environment exhibit the same basic pattern of damage (Table 2). Intrinsic effects were detected only in the three environments containing hard substrata, where the composition of shell supply modulates the strength of the taphonomic signature: epifaunal shells and thick shells exhibit the same basic patterns of postmortem damage as their infaunal and thin-shelled counterparts, but do so with significantly higher frequency. The larger the proportion of epifaunal and thick shells, the more strongly the taphonomic signature of the environment is registered in the total death assemblage.

Relative Importance of Different Intrinsic Factors.—The intrinsic factors that are most strongly linked to high frequencies of shell damage are epifaunal life habit and shell thickness (>0.5 mm), which covary in Bocas death assemblages: 72% of epifaunal shells are also thick, whereas only 41% of infaunal shells are thick (Table 1). Mineralogy does not appear to be a factor: only 36% of epifaunal shells are composed of foliated calcite (an additional 11% are composed of prismatic calcite; data from Table 1). In general, shell damage within Bocas bivalve assemblages is not linked to shell mineralogy: among low-organic microstructures, foliated calcite conveys a greater likelihood of shell damage only in the relatively high-energy *Halimeda* gravelly sand environment (Fig. 6A,B).

Our results suggest that high-organic microstructures may be more of a preservational liability among infaunal taxa (or in fine-grained substrata) than among epifaunal taxa (or in coarse and hard substrata), but these

microstructural types are uncommon in all environments and much larger sample sizes are needed to test the effect with confidence. In future studies, the additional sampling effort would be well worthwhile: although high-organic microstructures are relatively uncommon in Recent molluscan faunas, they constitute an increasing proportion of bivalve faunas back into the fossil record.

Causes of Intrinsic Effects.—We attribute the higher frequency of damage among epifaunal shells to their death above the sediment-water interface, which creates an opportunity for postmortem modification immediately after death, especially by encrustation and boring, that typically does not exist for infaunal shells. It is interesting that, even in hard-substrate settings where all shells probably undergo multiple cycles of burial and exhumation on the seafloor, and where some epifaunal individuals may even be buried alive, epifaunal shells are still damaged more frequently than infaunal shells. This suggests that taphonomic processes are operating rapidly, such that even a short initial delay in burial can launch epifauna significantly ahead of infauna in the accumulation of taphonomic damage. Our ongoing experiments in Caribbean Panama suggest in fact that significant damage occurs within months of exposure in all environments (Best and Kidwell 1996; Best 1998).

The higher frequency of damage to thick shells may reflect the preferential selection by infesting taxa of the most durable (bulky) shell substrata in a local death assemblage, regardless of whether these shells are exposed at the sediment-water interface immediately after death or at some later time. Highly selective settlement behavior by encrusting and

boring organisms is well documented in both the ecological and paleontological literature, including selective infestation of the thickest portions of live and dead shells. This kind of behavior might also contribute to the high damage frequencies observed among epifaunal shells if, for reasons of shell microstructure, infesters preferentially colonize the interiors of epifaunal shells (e.g., microbial preference of nacre over porcellaneous aragonite observed by Glover and Kidwell [1993]).

The higher frequencies of damage among epifaunal and thick shells, and the lack of consistent taphonomic differences between calcitic and aragonitic shells, may seem to contradict timed-release experiments (e.g., shells tumbled with abrasive, submerged in acid, exposed to infesters [Chave 1964; Driscoll 1970; Peterson 1976; Flessa and Brown 1983; Glover and Kidwell 1993]). Such studies consistently find that different shell types accrue damage and disintegrate at different rates, and that the classes of bivalve shells having *lowest* reactivities are calcitic (all of which are epifaunal species), thick (small surface area to mass ratio), low in intraskeletal porosity, low in microstructural organic content, and large bodied. However, in time-averaged assemblages, where shells have been supplied throughout an interval of time rather than at only a single moment, the rapid destruction of weak shells should result in (1) "durable" subsets of taxa exhibiting *more* rather than less damage than fragile subsets (basic pattern observed in Bocas) and (2) durable subsets having greater degrees of time-averaging (i.e., the widest range in shell age-since-death). This latter point has not yet been tested in Bocas via direct-dating. Elsewhere, direct-dating of Holocene bivalves has shown that, although damage accrues episodically rather than continuously, older shells within time-averaged assemblages are more consistently in poor condition than younger shells (Meldahl et al. 1997).

Thus, in addition to the probable effects of (1) an initial window of postmortem exposure on the seafloor not shared by all shell types and (2) preferential attack on some shell types by taphonomic agents, the observed high damage to epifaunal and thick shells might also reflect (3) some degree of disharmonious time-averaging (*sensu* Kowalewski 1996), with some bi-

ological subsets of the death assemblage (durable epifaunal and thick-shelled taxa) having greater average shell age-since-death than others.

Comparison with Previous Studies.—Parsons and Brett (1991) also noted that epifaunal shells had higher levels of damage than infaunal shells in reef sediments, but because their data combined damage to both shell exteriors and interiors, the taphonomic contribution to the pattern was unclear (the exterior surfaces of epifaunal shells may be damaged during life). Within a series of pure-carbonate subtidal environments of southern Florida, Dent (1995) also reported higher levels of encrustation and boring for two epifaunal target taxa (chamid bivalves, cerithiid gastropods) than for an infaunal taxon (tellinid bivalves), whose damage was limited to edge alteration, surface degradation, and abrasion (damage to all surfaces pooled).

Studies that target damage to single taxa aim either to control the variable of shell supply on taphofacies or to use that taxon as an exemplar of a class of shells, and thus comparisons to our results are not straightforward. These studies also pool damage to shell exteriors with data on shell interiors, and thus are testing the overall condition of shells rather than strictly postmortem damage. Most studies find that target taxa collected from different environments have different taphonomic signatures, demonstrating that extrinsic factors can be significant (Meldahl and Flessa 1990; Fiege and Fürsich 1991; Cutler 1995; Pandolfi and Greenstein 1997).

In a single environment, however, these studies show that different target taxa can yield very different frequencies and profiles of damage, suggesting the potential for significant intrinsic supply effects. Dent (1995), for example, found that the damage profiles of one epifaunal target taxon were invariant across south Florida environments (chamid bivalves; probably allochthonous in some environments), a second epifaunal taxon (gastropod *Cerithium*) closely resembled the total death assemblage in each environment, and an infaunal target taxon (tellinid bivalves) varied in damage among environments but diverged from the total assemblage. Our anal-

ysis of complete subsets of taxa reveals the magnitude of these potential supply-effects and finds that the intrinsic nature of local bivalve communities has only quantitative rather than qualitative effects on overall death assemblage condition in tropical subtidal environments.

Our study does not contradict earlier work, but is the next logical step, and it underscores the importance of testing for relative effects of intrinsic and extrinsic factors, to determine if, for example, intrinsic factors are more important in some depositional systems than in others. Biological subsets of assemblages, defined by life habit or by construction (e.g., pelmetazoan study by Meyer et al. 1989), are probably more meaningful units of comparison than single taxa for such analyses, and would maximize the confidence of extrapolating results into the fossil record. This approach could be used in any setting but is especially practical in tropical systems where species richness and equitability are typically high, making it difficult to acquire statistically meaningful numbers of single target species in all environments.

Conclusions

Analysis of bivalves from Caribbean Panama indicates that in each of the environments studied, all biological subsets exhibit the same pattern of damage (rank order of damage types) and differ only in the absolute intensity of that damage. This result has several advantages for taphofacies analysis. First, it means that shell supply has a quantitative rather than a qualitative effect on taphofacies—the nature of the local bivalve community modulates the intensity of the damage style, not its fundamental pattern. In this situation, a residual assemblage of calcitic taxa or molds of thick shells would yield the same basic environmental signature as the complete bivalve fauna, were it preserved. Second, some subsets of the fauna, particularly epifauna or thick shells, could be targeted for facies analysis because they register taphonomic differences more strongly than other death-assemblage components.

From a paleobiologic perspective, it is not clear whether these within-assemblage differ-

ences in the intensity of damage (seen only in hard-substrate environments) signify differences in degree of time-averaging (range in age-since-death of individuals), exposure time (which may be \leq age-since-death), selectivity in attack by taphonomic agents, or some combination of these factors, which have different consequences for bias in paleobiologic information (loss in time resolution, versus modification of species' relative abundances). These issues are under investigation using a combination of field experiments and direct-dating (Best unpublished; Best and Kidwell unpublished; Best et al. unpublished). The implication is clear, however, that these subsets of the faunal record, although from the same environment, are probably not iso-taphonomic in terms of bias.

The next question is the generality of our results. Existing data sets on the condition of death assemblages in other study areas could be dissected into biological categories like those here, and thus might rapidly yield comparable information on the effect of shell supply in other settings. A priori, it is difficult to anticipate how—or whether—patterns of damage accrual in death assemblages vary geographically without some form of empirical data. For example, extrinsic environmental effects may dominate over much of the tropical shallow-marine seafloor because, as in Bocas, biological agents play an extremely large and aggressive role in shell destruction (encrusters, borers; also elevated rates of microbial maceration? Best and Kidwell this issue). On the other hand, within the Bocas study area, it is hard-substrate environments that host death assemblages with the greatest damage. Although this reflects a combination of extrinsic and intrinsic factors (frequent reworking, low net burial rates, abundant epifauna), some of these same conditions would apply on cobble-, rock-, and shell-grounds in higher latitudes, and in fact molluscan assemblages there can comprise highly damaged material (e.g., Wilson 1982; Young and Nelson 1988). That is, among shallow subtidal environments, perhaps grain size or low net sedimentation, and the other biological and physical conditions linked with it, are the key variables rather than depositional system per se

(carbonate versus siliciclastic) or latitude and climate.

A systematic exploration of major environmental settings, whose assemblages are dissected into intrinsic biological categories such as life habit and shell construction for analysis, is thus required to determine the overarching patterns of taphonomic damage. Accompanied by field and laboratory tests of causality, including how damage and bias correlate, we will then be better positioned to extrapolate back into the fossil record, where the proportions of benthic life habits and hard-part types have changed over evolutionary time.

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