

Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. I. Environmental variation in shell condition

Mairi M. R. Best and Susan M. Kidwell

Abstract.—Contrary to the geological stereotype of pure-carbonate reef platforms, approximately 50% of shallow shelf area in the Tropics is accumulating siliciclastic and mixed siliciclastic-carbonate sediments. Taphonomic characterization of these settings is thus essential for assessing variation among major facies types within the Tropics, as well as for eventual comparison with higher-latitude settings. Our grab samples and dredge samples of bivalve death assemblages from nine stations in five subtidal habitats in a large marine embayment of Caribbean Panama (Bocas del Toro) provide the first actualistic information on the taphonomic condition of shells in Recent tropical siliciclastic sediments. Focusing on unambiguous damage to bivalve shell interiors, we found that the quality of shell preservation in fine-grained siliciclastics is superb: commonly $\ll 10\%$ of specimens are affected by encrustation, boring, edge-rounding, and fine-scale surface alteration via dissolution, microbioerosion, and maceration. Pure-carbonate and mixed siliciclastic-carbonate environments containing hard substrata (patch reefs, *Halimeda* gravelly sand, mud among patch reefs) contain higher numbers of more severely damaged shells (generally $>25\%$) and also higher diversities of fossilizable encrusters and borers. Disarticulation and fragmentation are pervasive across all environments and are probably related to predation rather than to postmortem processes. As in other shallow subtidal study areas, the taxonomic compositions of death assemblages have not been homogenized by postmortem transport but show high spatial fidelity to the distribution of living species. Assemblages from the five sedimentary environments have distinct taphonomic signatures, but the strongest differences are between the two fine-grained, exclusively soft-sediment siliciclastic environments on the one hand and the three environments containing hard substrata on the other. Experimental tests for rates and agents of damage, still in progress, indicate that the most critical environmental variables are exhumation cycles and burial rate. Bivalve death assemblages from Bocas del Toro demonstrate that damage levels in tropical fine-grained siliciclastic environments are much lower than in closely associated reefs and algal sands, and suggest a less filtered record of biological information.

Mairi M. R. Best and Susan M. Kidwell. Department of the Geophysical Sciences, University of Chicago, Chicago, Illinois 60637. E-mail: mmrbest@midway.uchicago.edu and skidwell@midway.uchicago.edu

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Introduction

One of the major unknowns in marine taphonomy is the effect of climate and latitude on patterns of skeletal preservation. The physical condition of death assemblages has been studied extensively in temperate latitudes, and analogous information for tropical carbonates has grown rapidly, especially in the last decade (mollusk studies by Ekdale 1977; Tudhope and Scoffin 1984; Miller 1988; Tudhope 1989; Parsons 1989, 1993; Miller et al. 1992; Dent 1995, 1996; Perry 1996, 1998; echinoderms by Nebelsick 1992, 1995; Llewellyn and Messing 1993; Nebelsick et al. 1997; reef corals by Pandolfi and Minchin 1995; Greenstein and Moffat 1996; Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997a,b). However, although carbonate platforms and other sites of predominantly carbonate accumulation constitute the geologi-

cal stereotype for low-latitude settings, they occupy only about half of shallow tropical shelf area, for example occupying $\sim 45\%$ in American Tropics (Best 1998a). Siliciclastic and mixed siliciclastic-carbonate sediments characterize the remaining shelf area. Tropical siliciclastics may differ from temperate-latitude analogues in total input and seasonality of organic matter; rates and seasonality in bioturbation and, thus, sediment aeration; types and quantities of dissolved ions (tropical subaerial weathering); and the composition, rate, and timing of skeletal carbonate input (e.g., possible latitudinal differences in shell robustness, body size, productivity). However, actualistic taphonomic data are lacking and even sedimentological information is limited for such environments, despite their obvious importance today and in the geologic past.

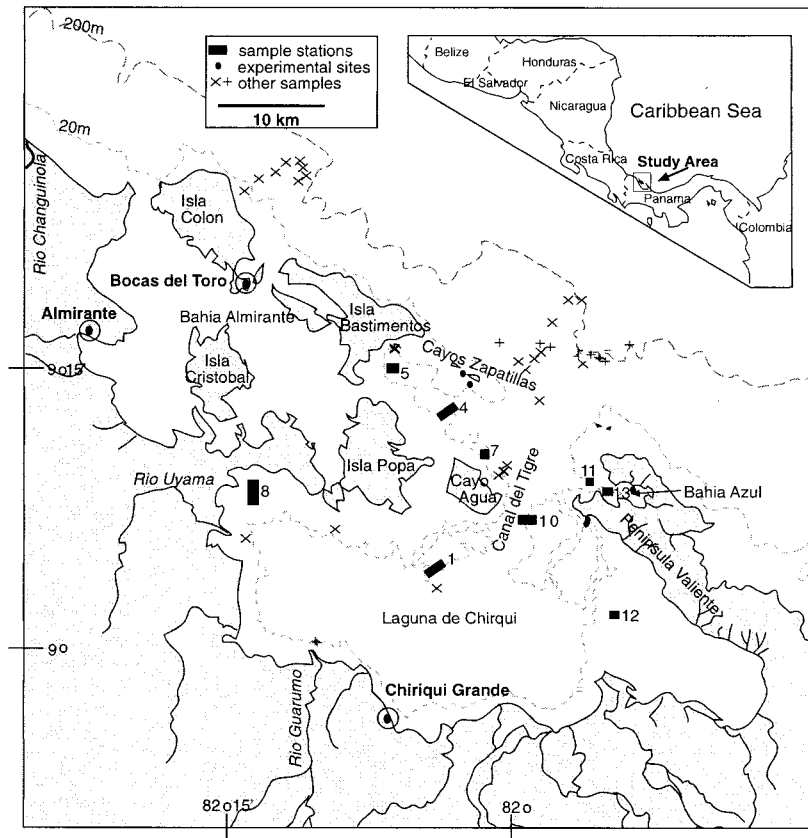


FIGURE 1. Bocas del Toro embayment of Caribbean Panama, showing location of sampling stations and regional geomorphology. Polygons enclose sampling area of multiple grabs and dredges per station.

There are many reasons to suspect fundamental differences in the taphonomy of macroinvertebrate hard parts within tropical siliclastic and carbonate sediments. Siliclastic sediments are typically more abrasive, have more turbid overlying waters, and, owing to the presence of iron and other metals, may have less-saturated pore-water chemistries than in pure carbonate sediments (e.g., Aller 1982; Walter and Burton 1990; Green et al. 1996; but see Aller et al. 1996 for evidence of oversaturation due to iron). Siliclastic sediments also typically support different benthic communities of shell producers and modifiers. The net effect of these physical, chemical, and biological factors on shell preservation in tropical siliclastics is unknown. Some of these environmental attributes might convey advantages to shell preservation in siliclastics (e.g., less light penetration of water column to support boring algae), whereas others

are expected to be disadvantageous. For example, oxidation of pyrite, which lowers pore-water pH and promotes shell-carbonate dissolution in temperate latitudes (Aller 1982), could operate at even higher rates in the Tropics.

To examine these issues, we are investigating siliclastic and carbonate subtidal seafloors along the Caribbean coast of Panama through taphonomic evaluation of death assemblages, experimentation with arrays of tethered shells, sediment analysis, and pore-water geochemistry (Best and Kidwell 1995, 1996; Best 1996a,b, 1998c; Ku and Walter 1998; Best et al. 1999). Here, we report results on bivalve death assemblages from the Bocas del Toro area of Panama (9°N), a region of extensive, primarily siliclastic sedimentation in a relatively deep (37 m), geomorphically complex embayment (Fig. 1). Taphonomic analysis focused on bivalves because of their abun-

dance in both reef and nonreef tropical environments. The Caribbean coast of Panama provides sedimentary and climatic conditions typical of the American Neotropics, and its modern fauna and fossil record are of particular interest to studies of marine biodiversity and its response to Neogene uplift of the Panama Isthmus (Jackson et al. 1997).

To identify postmortem damage unambiguously, our analysis focuses exclusively on damage to shell interiors. Most previous taphofacies studies have summed damage to shell interiors and exteriors, some of which may be acquired during the life of the shell producer.

Geologic Setting

The Bocas del Toro embayment lies on the Caribbean coast of Panama near the Costa Rican border (Fig. 1) and is situated within the late Cenozoic back-arc basin of the andesitic volcanic arc that forms much of the Panamanian Isthmus. Outcrops of Neogene marine siliciclastic sediments, derived from the arc and now uplifted along a network of small faults (Coates et al. 1992; Seyfried et al. 1994), form a series of mangrove-fringed peninsulas and islands within the embayment. These faults are probably also a major control on local bathymetry (Greb et al. 1996). Windward cliffed shorelines are local sources of siliciclastic sediment, supplementing that derived from the mainland watershed, which reaches elevations of >2200 m. Along the coast immediately east and west of the Bocas embayment, the open Caribbean reef front is attached to the mainland and occupies the inner edge of a seaward-dipping shelf. Across the broad mouth of the Bocas embayment, the reef front is attached to bedrock islands in the west (Islas Colón and Bastimentos) and, in the east, continues as a series of carbonate sand keys on submerged horsts (Cayos Zapatillas) (Greb et al. 1996). A deep natural channel (Canal del Tigre) cuts across the reef front between Cayos Zapatillas and the mainland Península Valiente, which defines the eastern edge of the Bocas embayment.

Greb et al. (1996) surveyed the sedimentology and macrobenthic ecology of the shallow-water (<12 m) pure-carbonate environments

that fringe islands in the western sub-basin (Bahía Almirante; Fig. 1), including data on the Cayos Zapatillas reef platform. Sedimentologic and ecological information for the eastern siliciclastic-dominated portion of Bocas del Toro is limited to ecological surveys of foraminiferans and corals (Havach and Collins 1997; Guzmán and Guevara 1998a,b).

Hydrographic information for this part of the Caribbean coast is summarized by Greb et al. (1996). The prevailing regime is microtidal (0.3 m normal, 0.5 m spring tide), and the area lies outside Caribbean hurricane tracks. Although most of the Bocas embayment is protected by the outer line of bedrock islands and carbonate keys, wind-driven swells from the northeast typically sweep directly into Canal del Tigre, breaking on the north coast of Cayo Agua and the tip of Península Valiente (NE prevailing wind; storms from northwest during rainy season [Sadler et al. 1987]). These swells, combined with tidal exchange of a large volume of water in Laguna de Chiriquí (max. depth 37 m), create substantial currents through Canal del Tigre, especially at its narrowest segment along the eastern edge of Cayo Agua. A longshore current also sweeps the Bocas del Toro coastline from the northwest. Whereas a part of this current is apparently deflected into Bahía Almirante in the northwest (max. depth 24 m) (Greb et al. 1996), it is probably less important in the southeastern portion of the embayment where our work has concentrated.

Precipitation is strongly seasonal, ranging from virtually no rain in February and March to as much as 566 mm in November; the annual average is 3305 mm (Greb et al. 1996). Runoff during the fall rainy season, particularly from the Rios Guarumo, Guariviara, and Cricamola, delivers a large but as yet unquantified volume of fine siliciclastic sediments from the mainland. Sediment plumes off these rivers can extend >30 km and persist for several days after major rains (Best and Kidwell personal observations 1994, 1995, 1997). Visibility measured with a Secchi disk during a dry week in November 1994 was quite high (9–16 m; our data), with highest values on the windward side of Cayo Agua where oceanic waters enter the embayment via Canal del Ti-

gre. Water temperatures are also seasonal, with the mean shifting from 28.0°C during the May–December wet season to 26.6°C during the dry season off the Bocas coast (Sadler et al. 1987). In November 1994, we measured temperatures of 28.3°C throughout the water column in stations adjacent to Canal del Tigre (12–29 meters) and found warmer surface water in protected backwater stations (30.0°C surface, 0.6–1.1 degrees higher than bottom waters in 12–20 m depths). The exceptions were an extreme backwater station (station 12 in Fig. 1) where the entire water column had been heated to 30°C, and immediately off Rio Uyama (station 8) where the temperature stratification was inverted, probably because of freshwater outflow. These measurements are consistent with a larger hydrographic survey conducted in 1997 by L. D’Croze (unpublished.).

Methods

The eastern embayment and adjacent shelf of Bocas del Toro were sampled from the RV *Uracca* (Smithsonian Tropical Research Institute) in November 1994 to explore sediment types and molluscan assemblages at a range of depths and oceanographic facings. Sampling focused on areas >10 m both to take advantage of the vessel and to examine environments with stratigraphically significant records. Several subareas within the embayment were reoccupied for supplementary environmental information in June 1997, and at that time we also sampled two cross-shelf transects of the (siliciclastic) open shelf. This paper focuses on taphonomic data from the nine stations established within the embayment in 1994 (nine nonconsecutively numbered polygons in Fig. 1).

We collected at least three dredge samples and three Petersen grab samples at each station. Each was subsampled for sediment analysis, and the remainder was wet-sieved through a 2-mm mesh. Live specimens were removed and preserved in alcohol. Death assemblages were later wet-sieved with fresh water through 8-mm and 2-mm mesh. After air-drying, we determined the total volume of 2–8-mm and >8-mm grains and the percentage of bivalves, by volume and weight, within

the >8-mm fraction. Grain size (sedigraph and sieving), percent nitrogen, organic carbon, and carbonate (total weight percent nitrogen and carbon by elemental analysis, carbonate by digestion, following Verardo et al. 1990) were determined for bulk sediment samples by the Department of Geology, Northern Illinois University. For patch reefs, we tallied information from both loose bivalve shells within sediment and those attached to or wedged within dead coral rubble, which dominated these remotely collected samples; this contrasts with previous workers (Parsons 1993; Dent 1995), who sampled using SCUBA and examined shells exclusively from pockets of sediment within reef frameworks.

In preliminary subsamples, we found that some kinds of taphonomic damage in death assemblages were sensitive to shell size-class, as recognized previously in temperate death assemblages (e.g., Boekschoten 1966; Bosence 1979; but contra Davies et al. 1989; Staff and Powell 1990a,b), and thus we targeted the coarsest fraction (>8 mm) where levels of damage were thought to be greatest and where species identification would be most straightforward. The vast majority of the shells fell within a range of 8–20 mm. To facilitate organization of the database, and to allow information on specimens to be verified or augmented at a later date, we gave each bivalve shell or shell fragment a unique identifying number.

Interior surfaces of all bivalve specimens were examined by 10× microscope, and results for six major categories of damage are reported here: disarticulation, fragmentation, edge-rounding, and, based exclusively on shell interior surfaces, encrustation, nonpredatory boring, and fine-scale alteration of surface texture. For each category of damage, both the specific type and extent of damage per specimen were tallied (Table 1), following a protocol similar to that of other workers (e.g., Davies et al. 1989; Kowalewski et al. 1995). Results are presented as a damage profile (bar graph), summarizing the percentage of shells that display fragmentation (any degree), rounding of the commissure, presence of encrusters or borers, and relatively severe

TABLE 1. Data types per shell.

| Ecological information Genus/species | Minerology | Robustness | Life position | Attachment | Feeding strategy |
|---|--|--|----------------------------|---------------------------------------|--|
| According to a taxon list | aragonite | thin (<0.5 mm) | infaunal | free-living | filter feeder |
| Based on type specimens | calcite nacreous aragonite | thick (>0.5 mm) | semi-infaunal epifaunal | byssate cementar borer | mixed feeder chemosynthetic deposit feeder |
| Taphonomic information Fragmentation and disarticulation | Encrustation | Boring | Edge-rounding | Fine-scale surface alteration | |
| Valves articulated | no encrustation | no boring | unmodified edges | pristine | |
| Single whole valve | fine worm tubes | sponge | chipped edges | dull | |
| Large fragment (>20% valve) | serpulid/spirorbid | worm | rounded edges | chalky | |
| Small fragment (<20% valve) | agglutinated worm tube barnacle sheet bryozoan net bryozoan bivalve vermetid sponge coral <i>Homotrema</i> disk foram agglutinated foram calcareous algae brachiopod | bivalve root etching grazing bryozoan | thinned edges | pitted chalky and pitted eroded | |

fine-scale damage (either chalky and pitted, or eroded).

In our protocol, fine-scale alteration refers to various degrees of degradation of original luster; it may be due to any combination of microboring and other microbioerosion, partial dissolution of mineral crystallites, maceration of shell organic matrix, and physical abrasion, which require a scanning electron microscope (SEM) to distinguish (see Cutler 1995; Best and Kidwell 1996; Best 1998c; Best et al. 1999). This suite of damage types is grouped under the general category of "dissolution" or "corrosion" in many other studies. Because visible chalkiness can be produced by mantle anaerobiosis during the life of a bivalve (Crenshaw 1980), we tallied fine-scale alteration using only the portion of the shell interior outside the pallial line, an area not prone to the artifact of *in vivo* dissolution and characterized in a given species by a single microstructural type. This latter point is important, because styles and rates of fine-scale alteration are almost certainly a function of shell microstructure (i.e., the size, shape, mineralogy, and packing of mineral crystallites in organic matrix) (see Glover and Kidwell 1993) rather than of environmental conditions alone. Our subdivision of shell interiors into microstructurally and physiologically distinct anatomical sectors for taphonomic characterization contrasts with division into geometric sectors related to life position (e.g., Davies et al. 1989), which is most relevant for tallying damage to shell exteriors.

Sedimentary Environments

Our benthic surveys in the eastern two-thirds of the Bocas embayment indicate a mosaic of largely siliciclastic sediments with point sources of carbonate production (Table 2, Fig. 2). The geomorphic and hydrographic complexity of the embayment creates a mixture of low- and high-energy shallow-water environments. Windward shorelines of bedrock islands (including the western edges of Península Valiente) are characterized by pocket beaches of lithic sand interspersed with occasional small patch reefs and isolated corals. These foreshore and shoreface sands grade into muddy sand and sandy mud at 20–30 m

depth. The largest and most extensive patch reefs rise up from shallow muddy seafloors on the mangrove-rimmed lee sides of bedrock islands and in the muddy leeside of Cayos Zapatillas. These reefs include both live and relict material, are 5–10 m diameter, and have ~5 m relief. They are the primary sources of carbonate sediment, along with small meadows of occasionally coral-rich *Halimeda* gravelly sand (e.g., rimming the constricted portion of Canal del Tigre east of Cayo Agua) and carbonate sand and seagrass beds (leeside of Cayos Zapatillos). The embayment is dominated by green, gray, and brown clayey siliciclastic muds, which surround patch reefs and also form a low-relief plain in the innermost embayment (Laguna de Chiriquí). Muds increase in carbonate-mud content toward the open sea (to ~50%), and contain only a few percent skeletal debris >2 mm.

Five distinct sedimentary environments characterize waters >10 m (Table 2, Fig. 2). Three of these include hard substrata (patch reef, *Halimeda* gravelly sand, mud among patch reefs), and the other two present exclusively soft sediments (sandy mud, mud). Hard-substrata environments do not show a simple correlation with water energy—the largest patch reefs are in relatively protected lee areas, whereas *Halimeda* meadows are in current-swept areas—but all are in the shallowest-water portions of the embayment and are not found along the mainland shore. Environments are arranged in order of decreasing carbonate content and grain size in Table 2 and other figures.

Abundance and Taxonomic Composition of Bivalve Death Assemblages

Skeletal material >2 mm constitutes only a few percent by volume of sediments in the embayment (Table 2). However, virtually all of this material is taxonomically identifiable, and in siliciclastic sediments, bivalve shells and shell fragments constitute the majority. Consequently, relatively small (8–10 liters) samples of sediment yielded reasonable numbers of specimens >8 mm for taphonomic evaluation (2–15 specimens per liter of sediment) (Table 3). This abundance matches or exceeds that in other subtidal tropical sediments. For

TABLE 2. Sedimentary environment characterization.

| Environment | Water depth | Sediment color and grain size | Sediment composition | Characterization of benthos |
|--|----------------------------|---|---|---|
| Patch reef (stations 1 and 4) | 14–16 m (to tops of reefs) | small coral-dominated reefs, 5–10 m diameter, with 5 m relief above surrounding muddy sea-floor | carbonate hardground | mixture of live and dead corals, predominantly <i>Agaricia</i> (with <i>Siderastrea</i> , <i>Montastraea</i> , <i>Porites</i>) and other largely epifaunal taxa (rhynchonellid brachiopods, bryozoans, calcareous algae, vermetids, ropy sponges, <i>Homotrema</i> , <i>Spondylus</i> , and <i>Chiama</i>) |
| <i>Halimeda</i> gravelly sand (station 10) | 12–13 m | tan fine–medium–coarse carbonate sand (mostly <i>Halimeda</i> debris, some coralline algae and mollusk fragments), trace mud and sponge spicules; small patch reefs of corals and red coralline algae | no quantitative data for loose sediment, but $\gg 50\%$ carbonate; skeletal debris > 2 mm = 3.5% of bulk sample by volume | abundant clumps of live <i>Halimeda</i> , fleshy green algae, and both crustose and ramose red algae with abundant sand to gravel-sized calcareous debris; including shells of strombids and venerids; hermit crabs; area includes small reefs of primarily platy corals, especially <i>Agaricia</i> , crustose red algae, and other attached epifauna (<i>Spondylus</i> , <i>Barbatia</i> , and <i>Anomia</i> bivalves, bryozoans, rhynchonellid brachiopods) |
| Mud among patch reefs (stations 1, 5, and 8) | 14–20 m | light–medium green to grayish-brown mud, 4–6% $> 63 \mu$ (mostly shell gravel). Samples vary in proximity to patch reefs and in their content of coarse skeletal debris | mud size-fraction contains 18–52% carbonate; skeletal debris > 2 mm = 3–6% of bulk sample by volume | sparse to abundant molluscan shell material, mangrove debris; live lucinid and venerid bivalves, holothurians, priapulids; amount of reef-derived coral debris varies with proximity to patch reefs (see patch-reef facies description above) |
| Sandy mud (stations 7 and 11) | 24–29 m | greenish-gray sandy mud, 10–20% $> 63 \mu$ (mostly dark fine–medium mafic and lithic grains) | mud size-fraction contains 19–35% carbonate; skeletal debris > 2 mm = 0.3–1.0% of bulk sample by volume | coarser-grained site (station 7) has abundant large miliolid forams, hermit crabs, brachiopods, stomatopods, live sand dollars, mangrove debris, and mollusk shells; finer-grained site (station 11) includes dead spatangoids, strombids and other gastropods, mangrove debris, brachiurids, stomatopods, bivalve shells |
| Mud (stations 12 and 13) | 13 m | greenish-gray to brown soft clayey mud | mud size-fraction contains 20–30% carbonate; skeletal debris > 2 mm = 0.4–1.0% of bulk sample by volume | live cardiid, tellimid, corbulid, venerid, and pectinid bivalves and shrimp; mucus mats with shell debris, mangrove debris, spatangid debris, brachiurids, molluscan shells; in samples from sites nearer to mangrove shoreline (station 13), also dead <i>Spondylus</i> , <i>Chiama</i> , ramose corals, regular echinoids |

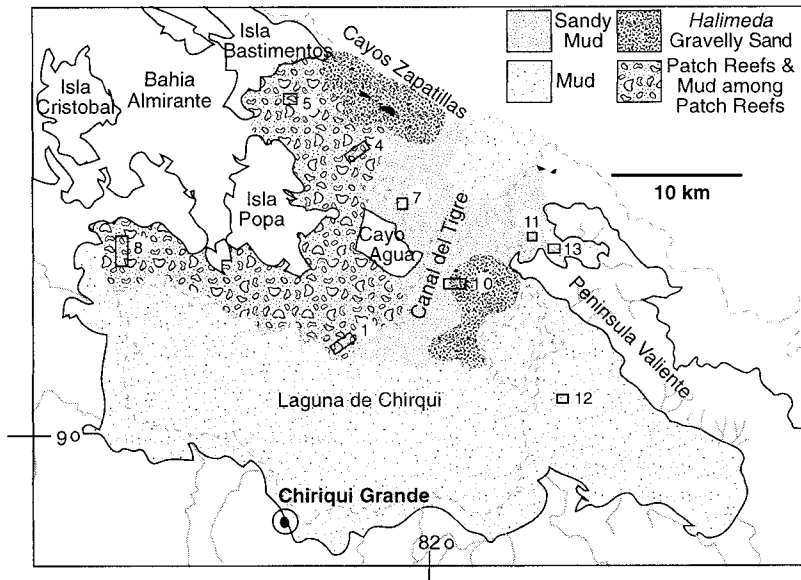


FIGURE 2. Distribution of sedimentary environments in Bocas del Toro study area showing dominance of siliciclastic sediments with point sources of carbonate. Subtidal areas in white are outside study; no data available.

TABLE 3. Percent abundance of bivalve life styles; d = dredge sample, g = grab sample.

Deposit feeders: several species of *Nuculana*

Chemosynthetic feeders: lucinids *Diplodonta*, *Codakia*, *Lucina*, and *Divaricella*

Mixed feeders: many species and several genera of Tellinacea

Suspension feeders (infaunal): venerids, cardiids, corbulids, *Glycymeris*, *Tagelus*, *Cardiomya*, and *Pandora*

Free-living epifauna: *Anadara brasiliana* and all pectinids except for one byssate *Chlamys*

Byssate epifauna: *Lima*, *Chlamys*, arcids, anadarids, *Barbatia*, *Pteria*, *Malvimmalleus*, *Pinna*, *Brachiodontes*, and *Gastrochaena*

Cementers and borers: several chamid genera, *Plicatula*, *Spondylus*, *Ostrea*, *Spengleria*, and *Lithophaga*

| Environment | Sample size (n) | No. of taxa | Infauna | | | | Epifauna | | |
|-------------------------------|-----------------|-------------|-----------------|------------------------|---------------|--------------------|----------------------|-------------------------------|----------------------|
| | | | Deposit feeders | Chemosynthetic feeders | Mixed feeders | Suspension feeders | Free-living epifauna | Byssate epifauna and nestlers | Cementers and borers |
| Patch reef | | | | | | | | | |
| 1-d3.0-0 | 48 | 8 | — | — | — | — | 2 | 31 | 67 |
| 1-d3.1-0 | 38 | 11 | — | — | 8 | 3 | 5 | 26 | 58 |
| 4-d19-0 | 49 | 14 | — | — | 6 | 22 | 14 | 24 | 33 |
| Halimeda gravelly sand | | | | | | | | | |
| 10-g44-0 | 101 | 26 | — | — | 13 | 20 | 3 | 16 | 45 |
| 10-d59-0 | 94 | 27 | — | 3 | 22 | 43 | 2 | 11 | 18 |
| Mud among patch reefs | | | | | | | | | |
| 1-d3.3-0 | 343 | 47 | — | 1 | 21 | 38 | 6 | 8 | 26 |
| 8-d36-4 | 100 | 27 | — | 18 | 22 | 41 | 7 | 2 | 10 |
| 5-d23-4 | 111 | 27 | 4 | 5 | 35 | 41 | 2 | 4 | 7 |
| Sandy mud | | | | | | | | | |
| 7-d35-1.1 | 73 | 12 | 37 | 5 | 33 | 11 | 11 | — | 3 |
| 7-d25-1.2 | 78 | 14 | 33 | 1 | 33 | 13 | 18 | — | 1 |
| 11-g49-0 | 98 | 10 | — | 3 | 66 | 24 | 6 | — | — |
| 7-g31-0 | 17 | 4 | 71 | — | — | 24 | 6 | — | — |
| 11-g47-0 | 44 | 10 | — | — | 61 | 36 | 2 | — | — |
| Mud | | | | | | | | | |
| 12-d63-2 | 109 | 9 | — | — | 26 | 73 | — | — | 1 |
| 13-d72-1 | 103 | 13 | — | 15 | 62 | 20 | 3 | — | — |
| 12-g61-0 | 147 | 13 | — | 1 | 32 | 65 | — | 1 | 1 |

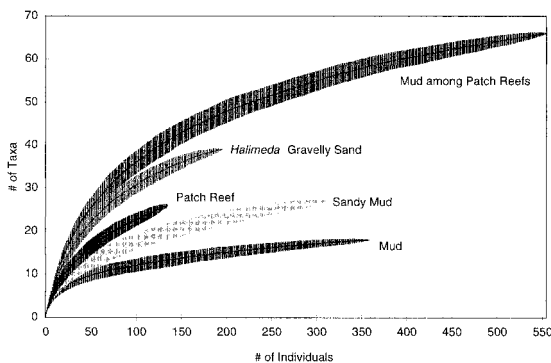


FIGURE 3. Cumulative sampling curve of taxa vs. individuals for samples pooled by environment. Each curve is the average of 200 bootstraps, with one standard deviation error indicated.

example, in the San Blas Archipelago of Panama, one liter of sediment in both carbonate and siliciclastic environments yields 1–18 identifiable bivalve specimens >8-mm (Best 1996a,b). Shell densities in pure-carbonate sediments were 0–30 specimens/liter in Madang, Papua New Guinea (>8 mm, bivalves only) (Best and Pandolfi 1992 and unpublished data), 1–25/liter in the Virgin Islands (>5 mm, combined bivalves and gastropods) (Parsons 1993), and an average of 38/liter in the Florida Keys (>2 mm, combined bivalves and gastropods) (Dent 1995).

The total number of bivalve species per sample ranged from 4 ($n = 17$ specimens) to 47 ($n = 343$) (Table 3, summarizing all processed samples). Pooled total diversity per environment ranged from 18 (mud) to 66 (mud among patch reefs) (Fig. 3). Cumulative sampling curves, pooled by environment, indicate that species richness per environment begins to level off (using maximum convexity on curve; see Heck et al. 1975; Sanders 1968) at ~8 for muds ($n \sim 30$ individuals), 14 for sandy muds ($n \sim 60$ individuals), 19 for patch reefs ($n \sim 70$ individuals), 29 for *Halimeda* gravelly sands ($n \sim 90$ individuals), and 36 for muds among patch reefs ($n \sim 100$ individuals) (Fig. 3). These data suggest that bivalve diversities in soft siliciclastic seafloors (mud, sandy mud) are significantly lower than those in carbonate-rich and hard substrata (*Halimeda* gravelly sand, patch reef). Moreover, a reasonable diversity of bivalve taxa is captured in quite modest samples. These estimates are almost

certainly conservative because the analysis was limited to the coarse fraction (>8 mm), the regional fauna is underdescribed, and some fragments were difficult to assign taxonomically to a species. Lumping of species is most significant among pectinids, oysters, and small infaunal species with few distinguishing features, but the large majority of specimens in samples could be assigned at least to the genus level, and virtually all could be assigned to ecological groups (Table 3).

These taxonomic richnesses are similar to single samples from other tropical subtidal environments, even those including finer size fractions of the death assemblage and reported as total richness rather than from a cumulative sampling curve. In San Blas Archipelago, total per-sample species richness ranged from 6 to 19 in siliciclastics (sample sizes of 40 to 89 individuals) and from 9 to 16 in carbonates (sample sizes of 33 to 44; Best 1996a,b, 1998c, and unpublished). In pure-carbonate environments, pooled bivalve richness ranged from 15 to 28 in Papua New Guinea (sample sizes of 73 to 158; Best and Pandolfi 1992, unpublished data), and per-sample total molluscan richness ranged from 8 to 39 in the Virgin Islands (sample sizes of 45 to 116; Parsons 1993) and from 17 to 75 in Yucatán (sample sizes of 39 to 3634, 3-mm mesh; Ekdale 1972, 1977).

Spatial Fidelity of Death Assemblages

In the study area, live mollusks (both bivalves and gastropods) were extremely rare at all stations, and so an evaluation of spatial fidelity via a live-dead comparison (e.g., Johnson 1965; Cadée 1968; Warme 1971; Miller 1988; Feige and Fürsich 1991) was not feasible: in washing 72 samples from the Bocas embayment and adjacent open shelf totaling ~2600 l sediment, we encountered only a few dozen live individuals >2 mm. Such low numbers are not unusual for single censuses of live mollusks in live-dead studies; many replicate samples in space and over time are generally necessary to build a rigorous database of molluscan diversity from living material alone (see Kidwell and Bosence 1991). Death assemblages can also be compared with other sources of information on the habitat preferences of

local fauna for the purpose of a live-dead comparison (e.g., Henderson and Frey 1986; Davies et al. 1989; Staff and Powell 1990a), but the Bocas fauna is insufficiently known to do this at the species level.

However, the spatial fidelity of death assemblages can also be assessed by evaluating taxonomic and ecologic compositions in light of the environment (e.g., Zuschin and Hohenegger 1998). In Bocas, the proportion of ecological groups in the bivalve death assemblages is significantly different at the 0.05 level for each of the five environments (Kolmogorov-Smirnov test of frequency; Sokal and Rohlf 1995) (Table 3), indicating that postmortem transport has not been so severe as to homogenize surviving death assemblages. Moreover, the relative proportions of these ecological groups are consistent with the physical characteristics of the collection station (Tables 2 and 3), suggesting the preservation of a strong signal from the original environmental distribution of these taxa during life. For example, the proportion of specimens from epifaunal bivalves requiring hard substrata (cementers, borers, byssate or nestling bivalves) is greatest in patch reefs, moderate in *Halimeda* gravelly sands (where there are both small patch reefs and live *Halimeda* for attachment), highly variable but generally lower in muds among patch reefs (depending on reef proximity), and virtually nil in sandy muds and muds. Infaunal bivalves are present in all but one sample (1-d3.0, patch reef), but numbers of individuals and diversity of infaunal feeding types are greatest in organic-rich sandy muds and muds.

Facies-Level Differences in Postmortem Damage

Disarticulation.—To account for possible disarticulation during collection, processing, and shipping, matching valves were counted as articulated, which, if anything, would produce an overestimate of articulation. Nonetheless, articulated valves are generally rare. In samples of soft substrata (sandy mud, mud), only 1–12% of specimens are articulated and these are limited to species with taxodont dentition (most commonly *Nuculana*). In settings that include hard substrata (patch reef,

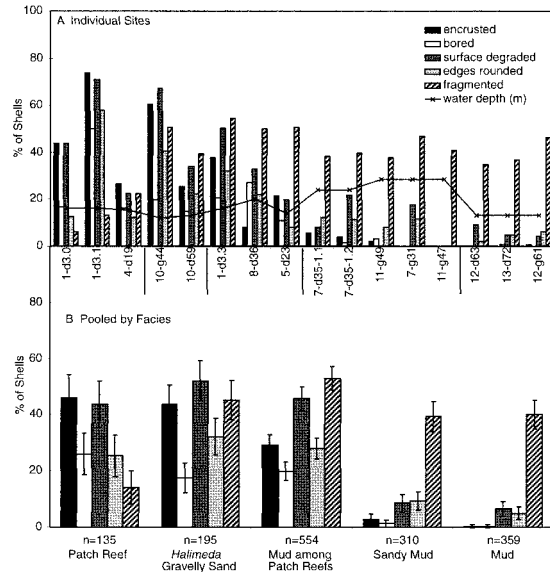


FIGURE 4. Taphonomic signatures of bivalve death assemblages based on percent frequency of shells with encrusters, macroscopic borers (nonpredatory), chalky and pitted or eroded shell outside the pallial line ("surface degraded"), rounded shell commissures ("round edges"), and fragmentation. A, Values per sample. Curve indicates water depth in meters. B, Values for samples pooled by environment; error bars are 95% confidence intervals.

Halimeda gravelly sand, mud among patch reefs), articulation is more common (e.g., 20–50% per sample from patch reefs), but is limited to specimens that are physically wedged within interstices of coral rubble (thus making the separation of valves difficult) and to species that have very thick ligaments or dentitions resistant to disarticulation (chamids, spondylids).

Fragmentation.—Levels of fragmentation are uniformly high across all environments (39–53% of bivalve specimens per sample; Fig. 4). The only exception is patch reefs (5–22% per sample), where low levels are attributable to the high abundance of cementing species (Table 3), which are represented primarily by intact valves still tightly attached to pieces of coral rubble.

Because shells can easily be broken during collection and processing, fragmentation (like disarticulation) is a problematic taphonomic variable. However, initial inspection of samples on deck and during gentle washing indicated that high levels of fragmentation were

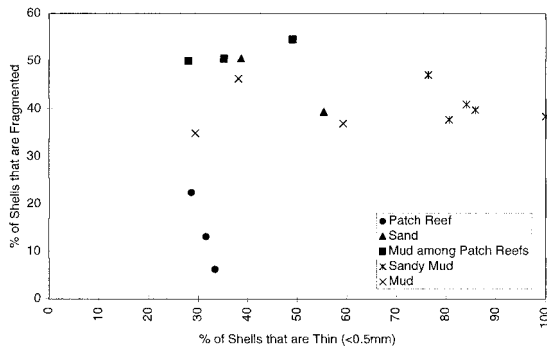


FIGURE 5. Percent frequency of fragmentation in death assemblages is not correlated with the frequency of thin shells or with environment.

not artifacts of sampling gear—grab and dredge samples had similar appearances—or of handling. Thus, although some additional fragmentation may have occurred during shipping, the qualitative pattern is probably robust (as argued by others for other study areas, e.g., Davies et al. 1989).

Fragmentation is not significantly correlated with water depth (12–29 m; Fig. 4A), relative water energy (inferred from sediment grain size and setting), or shell thickness (Fig. 5). Thus, although physical agents may contribute to fragmentation, they are not the primary or sole agents determining environmental differences. Predators and other organisms are the most likely agents of fragmentation in the low-energy muds, a conclusion supported by distinctive break patterns on shells (narrow invaginated breaks and chipped edges created by crabs and whelks; see Schäfer 1972; Cate and Evans 1994) and consistent with the observed abundance of shell-crushing rays and their feeding pits (Best personal observation on SCUBA).

Encrustation.—The percentage of bivalve shell interiors that are encrusted decreases with decreasing availability of hard substrata, from ~45% in patch reefs and *Halimeda* gravelly sands (no significant difference between these two environments, which both have extensive hard-substrata) to zero in muds (Fig. 4).

Rank orders of the different encrusting taxa are quite similar among environments, with calcareous tube-forming worms most abundant in all (serpulids and spirorbids), but sig-

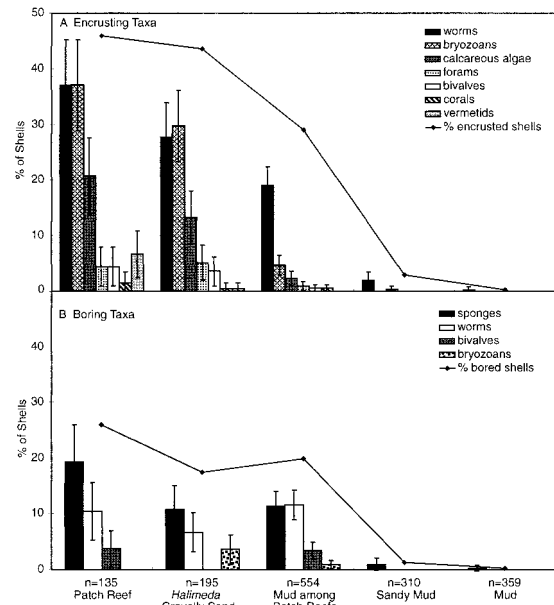


FIGURE 6. A, Percent frequency of shells that are encrusted and relative abundance of encrusters. B, Percent frequency of shells that are macroscopically bored and relative abundance of borers. Both graphs are pooled by environment with error bars showing 95% confidence intervals.

nificant quantitative differences do exist (Fig. 6A). Patch reefs and *Halimeda* gravelly sands have the highest diversities: calcareous tube-forming worms and bryozoans are most common, followed by calcareous algae; foraminifera, bivalves (chamids, ostreids), corals, and vermetids occur with lower frequency. In muds among patch reefs, worms overwhelmingly dominate other encrusting taxa; small numbers of bryozoans, calcareous algae, foraminifera, bivalves (chamids, ostreids), and corals are mostly associated with shells that were probably derived from nearby patch reefs (i.e., attached epifaunal bivalves). In all three of these hard-substrata environments, monospecific encrustations usually consist of runner bryozoans, suggesting that they are early colonists. In contrast, worms are virtually the only encrusters in bivalve death assemblages from exclusively soft substrata; barnacles, brachiopods, agglutinated worm tubes, and sponges (the latter two having poor preservation potential) occur only in trace amounts.

Within the study area, there is no correla-

tion between the level of encrustation and water depth (Fig. 4A), perhaps because the range was relatively narrow (12–29 m) and because some shallow-water muds have both low energy and relatively turbid overlying waters. The clearest environmental correlate of encrustation is the presence of hard substrata on the seafloor. The extent of hard substrata within an environment is difficult to quantify without detailed mapping using SCUBA, but nonetheless has a strong, essentially dichotomous effect: environments that include hard substrata all have assemblages with at least 20% encrustation levels, whereas exclusively soft substrata are characterized by encrustation levels of only a few percent, even when tested at the individual sample level (Fig. 4A). Water turbidity may be an additional factor, as light-dependent encrusters (calcareous algae, Foraminifera, corals) and those most sensitive to sediment smothering (bryozoans) occur primarily in nonmuddy stations.

Nonpredatory Boring.—Boring of shell interiors (examined at 10 \times) also covaries with the presence of hard substrata, ranging from 26% in patch reefs to zero in muds (Fig. 4B). Levels of boring are significantly higher in patch reefs than in the other two hard-substrate-bearing environments (*Halimeda* gravelly sand, mud among patch reefs), which are not significantly different from each other. The two soft-sediment environments (sandy mud, mud) have significantly lower boring levels but are not significantly different from each other.

Clionid sponges are the most frequent borers in all environments, and environments with hard substrata have the highest diversities of borers (Fig. 6B). Clionid sponges are followed or matched in frequency by spionid worms, followed by lithophagid bivalves and bryozoans. (Microborers are considered under fine-scale surface alteration.)

As with encrustation, there is no correlation between the frequency of bored shells and water depth within the study area (Fig. 4A), and the clearest environmental links are with the presence of hard substrata. All environments that include hard substrata have bivalve death assemblages with levels of boring 10% or higher, whereas environments that are exclu-

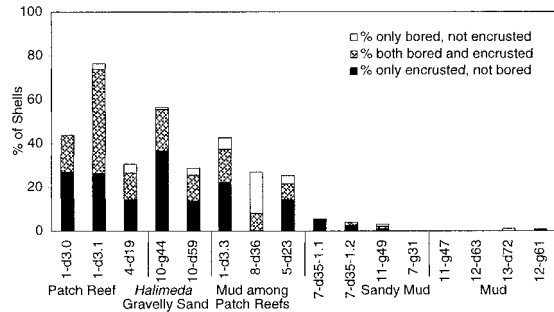


FIGURE 7. Association of macroscopic boring and encrustation on individual shells. Boring rarely occurs without encrustation, suggesting that encrusters are the first colonists of shell interiors.

sively soft have levels of only a few percent, even when tested at the level of individual samples. An additional environmental factor is indicated at station 8 (mud among patch reefs, sample 8-d36; Fig. 4A), where an anomalously high incidence of worm borings coincides with elevated nutrients from Rio Uyama (confirmed by L. D'Croz personal communication 1997). The fact that such overwhelmingly high levels of boring worms were not seen elsewhere suggests that, away from the immediate influence of a river, nutrient levels vary little throughout the lagoon (for an example of this in oligotrophic reefs see Kiene 1997).

Except at nutrient-rich station 8 (described above), boring levels are generally lower than encrustation levels (compare within Fig. 4B). However, the two types of damage are closely correlated, and in fact individual bivalve interiors are rarely bored unless they are also encrusted (Fig. 7). This suggests that encrusters are generally the first colonists of dead shells in our area, at least in stations of comparable nutrient regimes, and thus that shells that are merely encrusted might have been exposed at the sediment/water interface for shorter periods of time than those that are both encrusted and bored. We are presently testing this pattern in a series of experimental arrays in the Bocas embayment and in the San Blas Archipelago, Panama (Best 1998c).

Edge-Rounding.—Shells with rounded commissures (not rounding of the broken edges of shell fragments) are most frequent in environments with hard substrata, ranging from 32%

in *Halimeda* gravelly sand to 5% in mud (Fig. 4). There is no significant difference in levels among the hard-substrata environments, and only a marginal difference between the two exclusively soft-sediment environments.

Edge-rounding does not correlate with either water depth (Fig. 4A) or shell thickness. SEM examination (in progress) suggests algal or other micro-bioerosion and grazing of shell edges, perhaps by fish or echinoids, judging from "nibble" marks (Best and Kidwell 1996). Edge-rounding thus appears to be largely biological in origin.

Fine-Scale Alteration.—Shells whose interior surfaces outside the pallial line have lost their original luster and present a chalky, pitted, or eroded appearance (10 \times examination) are most common in environments with hard substrata (grand means 44–52%, reaching 71% in one sample) and lowest in exclusively soft-sediment environments (grand means 7–9%) (Fig. 4).

Although many causes are possible, initial SEM examination suggests that chalky and pitted textures were generated both by algal and fungal microboring and by microbial maceration of organic matrix, indicated by loosened crystallites, rather than by chemical dissolution (Best and Kidwell 1996; Best et al. 1999). Alteration can be quite high even in muddy, organic-rich sediments (e.g., ~20% in some individual samples from sandy muds; Fig. 4A), consistent with microbial attack, which is not impeded by shallow burial of shells (see Simon and Poulicek 1990).

Total Damage Profile.—As expected from trends in individual variables, the primary distinction among overall damage profiles (Fig. 4B) is between environments that include hard substrata (patch reef, *Halimeda* gravelly sand, mud among patch reefs) and those composed exclusively of soft sediments (sandy mud, mud). With the exception of fragmentation, which is high in all environments except patch reefs, death assemblages from exclusively soft substrata are virtually pristine, with significantly lower levels of all kinds of taphonomic alteration (<10% specimens altered, and commonly \ll 10% within individual samples). In contrast, environments containing hard substrata show high frequencies

of damage (>10% specimens altered, and generally >25%), and higher diversities of infesting taxa. Replicate samples from individual environments (Fig. 4A) yield consistent levels of damage for exclusively soft-sediment environments and heterogeneous results from hard-substrata environments. This is not unexpected given that the soft-sediment environments are far more homogeneous physically than the other environments. This difference in heterogeneity of taphonomic signature is being explored using rarefaction techniques (Best 1998b, unpublished).

Pair-wise comparison of environments within each of these two sets of environments reveals second-order differences in damage profiles (Fig. 4B). For example, muds have marginally less boring, encrustation, and edge-rounding than do sandy muds. *Halimeda* gravelly sand assemblages have marginally more edge-rounding and fine-scale surface damage, and less boring, than do assemblages from patch reefs, and mud among patch reefs differs from patch reefs only in having fewer encrusted shells. While these differences are sufficient to change the rank ordering of variables among these environments, the significances of these differences are marginal, and it is unwise to overinterpret them in light of the heterogeneity of the individual samples. The fundamental difference is between hard- and soft-substrata environments.

Discussion

Differences in Methods.—Quantitative comparison of trends in Bocas death assemblages with other studies is not straightforward. Studies diverge considerably in examining all mollusks, bivalves only, all species, or only a few target taxa, and also diverge in the size fraction, set of taphonomic variables, and method of scoring damage per specimen (Table 4). The robustness of taphonomic signatures to such differences in approach has never been fully tested, although individual studies have evaluated some aspects (e.g., effect of size fraction and of whole versus fragmented shells [Davies et al. 1989; Staff and Powell 1990b]; target taxa versus pooled data [Dent 1995, 1996]).

Our method diverges most strongly from

most previous studies by focusing exclusively on shell interiors, so that postmortem damage could be quantified unambiguously. This should not affect the comparability of our results for some variables, namely disarticulation, fragmentation, and edge-rounding. For other variables, we expect our observed frequencies will be equivalent to or lower than the frequencies we would have obtained by summing damage to both surfaces, making the Bocas dataset a conservative test of trends in postmortem damage. Other studies are consistent with this expectation. For example, considering only infaunal bivalves, which should be least sensitive to this methodological difference, Kowalewski et al. (1995) found no differences in damage to shell interiors and exteriors in Cholla Bay and San Felipe intertidal assemblages (Gulf of California), but tallied a larger number of pristine interior surfaces than exterior surfaces in North Sea intertidal assemblages. In Texas subtidal assemblages dominated by infauna, Staff and Powell (1990b) found no significant interior-exterior differences on the inner shelf, but Davies et al. (1989) did find greater abrasion and "dissolution" (= fine-scale alteration of diverse origins) on exterior shell surfaces in a nearby microtidal inlet. This differential damage may indicate selective attack of shell exteriors by taphonomic processes, but it may also have occurred during life, especially among infaunal species with little or no periostracum. This does not mean that tallying information from shell exteriors is not useful for facies discrimination, only that it is not unambiguously taphonomic.

Because it would have doubled the number of observations (already 41,931 for the 1553 specimens examined), we did not gather information on damage to exterior surfaces in Bocas assemblages, and thus do not know how large an artifact this common method might introduce, particularly in epifauna-rich assemblages (see concern of Parsons and Brett [1991] for reef-bearing study areas; see Best and Kidwell this issue). However, because we found highest damage in hard-substrata environments, just as Parsons (1993) did in her northeastern Caribbean study area using exterior as well as interior damage (see discus-

sion below), we suspect that combining exterior and interior shell damage may have only a quantitative rather than qualitative effect on perceived taphonomic trends.

Spatial Fidelity.—Differences among environments in the taxonomic composition of death assemblages, and the ecological consistency of assemblages with host sediments, suggest high spatial fidelity of molluscan remains at the facies-level within the Bocas del Toro embayment: postmortem transport is relatively minor both in distance and in quantities of shell moved out of life habitats. This result is consistent with the pattern emerging from other enclosed and open-marine environments, both siliciclastic and carbonate, and appears to be robust to the method of analysis and even to the perils of mobile shell-ingesting predators and intermittent high energy (e.g., Cadée 1968, 1984; Warme et al. 1976; Bosence 1979; Fürsich and Flessa 1987; Miller et al. 1992; Cate and Evans 1994; Flessa 1998; Anderson et al. 1998; see review by Kidwell and Bosence [1991]).

High spatial fidelity is also implied by the significantly different damage profiles seen for Bocas death assemblages from different environments (see reasoning of Parsons and Brett [1991]). Habitat-specific shell damage has been used elsewhere to recognize probable transport directions of sediments (Pilkey and Curran 1986) and the likely exotic origins of selected species in death assemblages (Davies et al. 1989), including hurricane-swept back-reef settings (Miller et al. 1992 reference to unpublished work; Perry 1996). In Australia's cyclone-affected Great Barrier Reef, Tudhope (1989) found only a few meters' transport of skeletal debris from patch reefs into adjacent soft sediments. We observe the same minimal off-reef transport around patch reefs in Bocas del Toro and San Blas Archipelago, Panama: shells from patch reefs are ecologically and taphonomically distinctive, and their abundance in surrounding muds diminishes to trace quantities within a few meters of the reef face (Best and Kidwell unpublished).

Biogenic Disarticulation and Fragmentation.—The high frequency of disarticulation and fragmentation in samples from quiet-water

soft sediments at Bocas suggests that this damage is largely biogenic rather than physical in origin. This and distinctive break patterns also suggest that this damage is generated largely by predators, rather than accrued during postmortem time-averaging on the seafloor. Similarly high values, attributed to predators and in many instances contrary to gradients in physical energy, have been reported from other low-energy settings (Cadée 1994; see review by Cate and Evans 1994). Feige and Fürsich (1991) reasoned that fragmentation was largely biogenic in their intertidal study area because it decreased across a gradient of increasing physical energy and decreasing sedimentation rate.

We attribute low fragmentation and disarticulation in Bocas patch reefs to the high proportion of species that are cemented to or otherwise firmly lodged in reef rubble in that local bivalve community. In contrast, Parsons (1993; Parsons and Brett 1991) found that fragmentation levels were *greatest* in reef (and beach) environments sampled in the Virgin Islands. We surmise that this difference results from her sampling areas of sand within reef frameworks, whereas we sampled the reef framework itself, and thus the damage profiles are from two different subhabitats.

Genesis and Significance of Other Damage.—All other kinds of taphonomic damage in the Bocas embayment—encrustation, postmortem boring, edge-rounding, and fine-scale surface degradation—are strictly postmortem in origin and are greatest in assemblages from patch reefs, *Halimeda* gravelly sands, and muds that receive skeletal debris from immediately adjacent reefs (Fig. 4B). High frequencies of such damage may correlate with hard substrata for many reasons, which need not be mutually exclusive. These include (1) intrinsic ecological factors, such as a larger proportion of epifaunal species, which, unlike infaunal species, necessarily experience a period of postmortem exposure on the seafloor before burial (see Best and Kidwell this issue), and (2) a host of extrinsic, covarying environmental factors.

The most likely environmental factor is greater exposure of death assemblages on patch reefs and coral-algal meadow seafloors,

due both to exhumation cycles and to slower net sediment accumulation rates. Water clarity probably also contributes to higher rates of encrustation in these settings. In contrast, we suspect that sedimentation (and therefore burial) rates in muddy environments are quite high in absolute terms, judging from burial of experimental arrays (e.g., up to 8 cm of sediment accumulated in one year on experimental shells deployed at the surface). Even in the absence of high sedimentation, shell exposure at the sediment-water interface would not be favored, because these muddy siliciclastic-rich sediments readily resuspend when touched by divers (Best personal observation on SCU-BA, in both Bocas and San Blas habitats). High organic contents (Table 2) also indicate that these muds have quite “fluffy” sediment-water interfaces unfavorable to many infesters, even under quiet water conditions. These benthic conditions would pertain even when Secchi-disk visibility in overlying waters is high, as they were during our fieldwork.

Elevated levels of fine-scale alteration in hard-substrata environments may reflect several different factors, operating both at the seafloor and during shallow burial: (1) greater exposure to light, fostering algal microboring and grazing-type bioerosion; (2) intermittently higher energy, providing more opportunities for physical abrasion; (3) stronger irrigation of pore waters in the coarser-grained sediments of these stations, fostering higher rates of sulfate reduction, greater reoxidation of reduced sulfide, and thus greater potential for carbonate dissolution in addition to any acidification from aerobic decomposition (see Walter and Burton 1990); (4) microbial attack of organic matrix, which may proceed in all settings (Simon and Poulicek 1990; Glover and Kidwell 1993), but which might be elevated in coarser-grained stations because of greater pore-water supply of oxidants (see Allison 1990; Walter and Burton 1990). SEM examination of shells from analogous environments in the Caribbean San Blas Archipelago of Panama (in progress) indicates that all of these except abrasion are probably factors in the fine-scale alteration associated with hard-substrata in the Bocas embayment. In muddy siliciclastic sediments, all of these factors would be re-

duced. Preliminary results indicate that the high iron content of siliciclastics in our San Blas study area fosters iron reduction and oversaturated pore waters (cf. Aller et al. 1996; Ku and Walter 1998, unpublished; Best et al. 1999), and this would cause an even greater taphonomic contrast between assemblages from hard-carbonate and soft-siliciclastic environments such as sampled in Bocas.

Finally, although edge-rounding has been used as a proxy for combined physical abrasion and chemical solution by many workers (Cutler 1987; Davies et al. 1989), based in part on tumbling experiments by Chave (1964), it is probably largely biological in origin in Bocas assemblages and dependent upon seafloor exposure. SEM examination suggests algal or other micro-bioerosion, exacerbated by grazing of shell edges (Best and Kidwell 1996). Moreover, in contrast to previous studies, edge-rounding in Bocas assemblages is not restricted to settings of prolonged or high-energy reworking or to thick shells (thought to better withstand such treatment).

The types of damage that are most common in hard-substrata death assemblages in Bocas are thus linked to seafloor exposure, either intermittent or continuous, and to the openness of sediments to solute exchange, rather than to high energy per se. Death assemblages in muds among patch reefs include skeletal debris that carries the taphonomic signature of these hard-substrate habitats. In contrast, postmortem damage to death assemblages from exclusively soft-sediment environments is virtually nil (Fig. 4B) and is primarily a microbial signature of sediment burial. The low frequency of encrustation and boring in these environments appears to reflect the limited exposure of shells above the sediment-water interface: infesting taxa occur in the same rank order as in hard-substrata death assemblages, simply at much lower frequencies, indicating a shared larval species pool (Fig. 6). The few shells that are exposed in soft sediments may in fact be more intensely colonized because of substratum limitation and lower grazing intensity (e.g., Jackson 1977; supported by experimental results of Best and Kidwell 1996; Best 1998c).

Broader Comparisons.—Working in pure-car-

bonate habitats of northeastern Caribbean, Parsons (1993; see Table 4 for methods) also found generally higher levels of damage in reef and high-energy sand environments than in bioturbated sands and muds, with the lowest damage levels in mud (Dent [1995] indicates that this mud includes considerable siliciclastic component). Encrustation and clionid sponge borings (the only endobiont tallied) were consistently high in all reef habitats and in rippled sands of the adjacent shallow shelf (1.5–22 m; 13–67% of shells, versus <2% of shells in muds and bioturbated sands <5.5 m; compare with our per-sample data in Fig. 4A). Fine-scale alteration (excluding rhizome etchings and polishing from abrasion) was also high in reefs and in sandy grass beds and beach sands (~40–95% of shells damaged), in contrast to shells in bioturbated sands and muds (0–8% of shells damaged, except for one station; compare with our Fig. 4). All of these environments would have experienced similarly high levels of water clarity, and thus differences in damage levels were attributed to differences in water energy, frequency of shell exhumation, and sediment accumulation rates, particularly where sedimentary veneers on hard substrata were especially thin. On the carbonate platform of the Florida Keys, Dent (1995) also found the highest damage levels in reef-framework and back-reef rubble habitats, and attributed this to more frequent physical reworking and exposure of shells. His single mud station (pure carbonate) was in a channel of presumed low net sedimentation, which was invoked to explain why shells exhibited more damage than found by Parsons (1993) in her more onshore, sediment-trapping mud habitat.

Workers in extratropical siliciclastic sediments have also underscored the importance of shell exhumation cycles and of low net sedimentation. High damage levels have been documented in mollusk shells from storm-reworked clastic-bypassed tidal inlets (Staff and Powell 1990a); from beaches, channels, and wave-influenced portions of macrotidal flats (Meldahl and Flessa 1990; Feige and Fürsich 1991); from clastic-starved nearshore areas between active coastal alluvial fans (Meldahl et al. 1997); from palimpsest offshore sands

TABLE 4. Comparison of results from quantitative taphofacies studies in modern environments, ordered latitudinally. Unless noted, all damage based on pooled observations on shell interior and exterior surfaces. n.s. = not specified. Codes for types of damage evaluated: Abr = abrasion, BI = biotic interactions (sum of bioerosion, encrustation, predation, etc.), Bio = bioerosion, Bor = boring (macroscopic), C = cracking, CL = color loss, Corr = corrosion, Disart = disarticulation, Diss = dissolution, Enc = encrustation, ER = edge-rounding, Exf = exfoliation, Frag = fragmentation, FSA = fine scale alteration (of ext = exterior & int = interior surfaces) LEO = loss of exterior ornamentation, MIB = microboring, Ppt = precipitation, R/L = ratio right/left valves, Rad = radular marks, RE = root etchings, SF = size frequency, TM = thinned margins

| Study area (author) | Environments sampled (depth) | Size fraction (>X mm) | Taxa | Types of damage | Method of scoring damage | Key results |
|---|--|-----------------------|---|---|---|---|
| Siliciclastic Environments | | | | | | |
| Skagerrak coast, Norway (Cutler and Flessa 1995) | Beach | 3 | infaunal and epifaunal bivalves | Bio, Corr (dissolution and maceration), Ppt | presence/absence of each type of damage on each shell (SEM) | majority of shells show microboring, half show signs of dissolution or maceration, and 10% show precipitation |
| North Sea coast, Germany (Kowalewski et al. 1995) | low-energy tidal flats and subtidal channels | n.s. | infaunal bivalve <i>Cerastoderma edule</i> | Abr, Bio, Enc, Frag, FSA (int and ext) | degree of each type of damage on each shell | generally moderate abrasion, very little fragmentation, and highly variable surface alteration |
| Cape Cod, Massachusetts (Meldahl and Flessa 1990) | salt marsh, inner flats, middle flats, outer flats, beach, subtidal (0-2.5 m), subtidal (2.5-10 m) | 6 | infaunal bivalve <i>Mercentaria mercenaria</i> | Abr, Bio, Corr, Enc, Frag | presence/absence of each type of damage on each shell | marsh and subtidal sands generally different damage from intertidal flats, but no simple trends |
| Sapelo Island, Georgia (Frey and Howard 1986) | offshore palimpsest sand (12-15 m) | 2.5 | entire molluscan death assemblage | Bor, CL, Enc, FSA | presence/absence of each type of damage on each shell | highest damage in sites with slowest sedimentation rates |
| San Luis Pass, Texas (Davies et al. 1989) | microtidal inlet (storm-dominated tidal delta) | 2 | 4 subsets of molluscan death assemblage, segregated by life habitats (inner shelf, beach/inlet, bay, eurytopic) | Abr, BI, Corr+MB, Disart, ER, Frag, SF | degree of each type of damage on each shell | damage linked to life habitats of species, accrued before transport to tidal delta; corrosion/microboring highest in eurytopic species, edge-rounding and abrasion highest in bay species |
| Texas coast (Staff and Powell 1990a) | microtidal inlet, inner shelf (15-22 m) | 4 | entire molluscan death assemblage | Abr, BI, Corr+MB, Disart, ER, Frag, R/L, SF | degree of each type of damage on each shell | damage decreases offshore, except corrosion; damage focused on shell fragments |

TABLE 4. Continued.

| Study area (author) | Environments sampled (depth) | Size fraction (>X mm) | Taxa | Types of damage | Method of Scoring Damage | Key results |
|---|--|-----------------------|---|--|---|--|
| Cholla Bay, Gulf of California, Sonora (Feige and Fürsich 1991) | salt marsh channel, inner flat, middle flat, middle channel, outer flat, outer channel | 3 | entire molluscan death assemblage and target genera <i>Protothaca</i> , <i>Chione</i> , <i>Dosinia</i> , <i>Tagelus</i> , <i>Cerithium</i> , <i>Cerithiidea</i> , and <i>Encope</i> | Bor, CL, Corr, Distart, Enc, Frag, LEO, R/L | degree of each type of damage on each shell | highest overall damage in channels; most damage increases seaward across flats as energy and biogenic reworking increase and as sedimentation rate decreases |
| Cholla Bay, Gulf of California, Sonora (Cutler 1995) | salt marsh, marsh channel, beach, spit with dunes, inner flat, middle flat, outer flat, rocky flat, subtidal rocky sand (1–5 m) | 6 | infaunal bivalves <i>Chione fluctifraga</i> and <i>Chione californiensis</i> | Abr, Corr, MB, Rad, RE | presence/absence of each type of damage on each shell | highest overall damage in spit; microboring dominates all except beach, where abrasion dominates; other damage types have limited distributions |
| San Felipe, Gulf of California, Baja California (Kowaleski et al. 1994) | modern chenier, submodern chenier, fossil chenier | 12.5 | infaunal bivalve <i>Mulinia coloradensis</i> | Bio, C, Enc, ER, Exf, Frag, FSA (ext. vs. int.) | degree of each type of damage on each shell | damage increases with geologic age and is greatest for shells sampled from chenier surface |
| Bahía Concepción, Gulf of California, Baja California Sur (Meldahl et al. 1997) | intertidal mangrove, nearshore (1–5 m), nearshore (5–20 m), offshore mud (>20 m), nearshore bioclastic sand | 15 | infaunal bivalve species | Bor (predatory + postmortem, incl. MB), CL, FSA (int), LEO, TM | each shell interior scored according to overall damage profile (4 grades of damage) | highest overall damage in shallowest water; among nearshore sites, highest damage in areas of slowest sedimentation |
| Pure-carbonate environments Florida Keys (Dent 1995, 1996) | onshore-offshore transect of Florida shelf: grass beds, sands, reef hardgrounds+rubble (1–7 m), plus 2 sand and hardground fore-reef sites (21–33 m) | 2 | 15 most abundant molluscan species in study area (of 386 total) | Abr, Bor (sponge only), CL, Enc, ER, Frag, FSA | degree of each type of damage on each shell | damage on reef is greater than in all other environments with the exception of fragmentation and color loss |

TABLE 4. Continued.

| Study area (author) | Environments sampled (depth) | Size fraction (>X mm) | Taxa | Types of damage | Method of Scoring/Damage | Key results |
|--|---|-----------------------|-----------------------------------|---|--|---|
| St. Croix, Virgin Islands, and Mona Island, Puerto Rico (Parsons 1989, 1992, Parsons and Brett 1991) | beach, mud, bioturbated sand, grass bed, sand pockets within patch reef, backreef, forereef, algal sand on open shelf hard-ground | 5 | entire molluscan death assemblage | Disart, Frag, Enc, Bio, RE, ER, Abr, CL | degree of each type of damage on each shell | highest overall damage in reefs and in beach sand, least damage in mud; reef facies not distinguishable from each other, but distinct from all other facies |
| Both siliclastic and carbonate environments | | | | | | |
| Bocas del Toro, Caribbean Panama (this paper) | sandy mud (silici), mud (silici), mud among patch reefs, patch reef, <i>Halimeda</i> gravelly sand | 8 | all bivalve species | Disart, Frag, Enc, Bor, ER, FSA (int.) | degree of each type of damage on each shell interior | highest damage in environments with hard substrata |

(Frey and Howard 1986); and, within chenier plains, from relatively old shell ridges that have suffered greatest meteoric exposure (Kowalewski et al. 1994) (Table 4). In the most relevant subset of subtidal muddy sediments, damage levels (based on both shell exterior and interior surfaces) are only slightly higher than those we observed in tropical siliclastic muds of the Bocas embayment. For example, between fair-weather and storm wave base on the Texas shelf, 91–98% of bivalve shells 4–12 mm were disarticulated, 16% were fragmented, 16% had significant fine-scale alteration (“major dissolution”), and 8–13% were encrusted or bored (latter figure for pooled bivalves and gastropods) (Staff and Powell 1990b; compare with our Fig. 4B). In offshore siliclastic muds of Bahía Concepción, preservation of bivalve death assemblages is consistently “good” to pristine, with >50% of specimens in “excellent” condition in all samples (color retained, no postmortem infestation, no edge alteration, may have some loss of luster) (Meldahl et al. 1997).

The excellent condition of shells from siliclastic muds in Bocas del Toro is not unique within the Tropics, as we are finding similarly well-preserved material from subtidal siliclastic muds in the San Blas Archipelago in eastern Panama (Best 1996b, 1998b,c). In the absence of *pure-carbonate* muds within the Bocas study area, it is not possible to isolate the effects of sediment composition on the one hand from sediment grain size and its physical environmental correlates on the other. Nonetheless, the differences in damage profile would be difficult to explain by sediment composition alone, so we feel confident that sediment composition is probably of only secondary importance among the set of environments examined in Bocas. The effect of sediment composition can be tested more straightforwardly in the San Blas area, where both siliclastic and pure-carbonate muds are present. In our preliminary data from San Blas, bivalve shell condition is poorer in pure-carbonate muds, primarily because of greater fine-scale surface alteration (Best et al. 1999 and unpublished). Such differences in sediment composition may in fact explain in part why Dent (1995) found that shells from his

pure-carbonate mud in Florida were in poorer condition than shells from Parsons's (1993) apparently impure muds in the Virgin Islands.

Conclusions

These results from Bocas del Toro constitute the first taphonomic characterization of molluscan death assemblages in Recent tropical siliciclastic sediments and can be compared with assemblages from pure-carbonate hard substrata in the same back-arc embayment, broadening the actualistic database for stratigraphically significant shallow-marine environments. To the advantage of taphofacies analysis in analogous fossil records, bivalve shells are relatively abundant, death assemblages have not been homogenized by postmortem transport, and each environment yields a distinctive damage profile. Between-sample variation is high within the physically heterogeneous hard-substrata environments, however, requiring greater pooling of data. The most distinct differences are between hard-substrata environments (patch reef, *Halimeda* gravelly sand, mud among patch reefs) and exclusively fine-grained, soft-sediment environments (sandy mud, mud), with the latter characterized by superb shell preservation. Because we only tallied damage to shell interiors, these differences are unambiguously taphonomic (postmortem) in origin.

Tests to determine rates and specific agents of damage are still in progress. However, the primary environmental (extrinsic) controls on damage are probably differences in exhumation cycles and burial rate, given the dependence of the most common kinds of shell damage on seafloor exposure. In hard-substrata environments, residence times at or very near the seafloor probably depend upon the frequency of physical reworking (relatively high in *Halimeda* gravelly sands but less so in leeward patch reefs) and the thickness of the sedimentary veneer (i.e., sediment available to bury shells; not great in either environment). In muddy substrata, we suspect damage levels are kept low by high rates of net sediment accumulation, low frequency of physical reworking of shells, and easily (e.g., tidally) resuspended sediments at the seafloor that would rapidly coat and effectively bury

shells upon death (for rare epifauna) or exhumation (including exhumation by burrowers). The only significantly non-zero taphonomic damage to shells in these exclusively soft-sediment environments, aside from perimortem disarticulation and fragmentation, is fine-scale alteration of shell interiors and commissural rounding. This alteration is probably largely microbial in origin and can proceed during shallow burial within anaerobic sediments.

Regardless of cause, the excellent condition of shells in assemblages from muddy tropical siliciclastic sediments suggests a less filtered record of original biological input than in assemblages from closely associated reefs and algal meadows. Low damage levels suggest that taphonomic processes have operated at very low intensity, thereby causing little differential destruction of species (i.e., little bias), and/or that sedimentation rates are very high, resulting in little time-averaging. Such optimistic extrapolations require testing before application to the fossil record, but preliminary results from experimental shells suggest that rates of damage for buried shells in all environments are quite low, with at most a few percent weight loss in a 27-month period and all of this achieved within the first 12 months (Best and Kidwell 1996; Best 1998c; Best et al. 1999). All types of damage show higher levels in hard-substrata assemblages, but these also include types that accrue only during exposure. Although key rates are yet to be quantified, given such significant differences in shell condition, the compositions of assemblages from these contrasting sets of facies (or alternating shale and limestone beds) are not likely to be isotaphonomic, that is providing the same qualities of paleobiologic data. However, within each of the two sets of environments tested here, assemblages are quite similar in condition, and thus might be accepted as taphonomically equivalent sources of paleontologic information.

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