

# Taphonomic Feedback in Miocene Assemblages: Testing the Role of Dead Hardparts in Benthic Communities

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*The accumulation of dead hardparts can directly influence the structure and dynamics of benthic communities by changing the physical characteristics of the sea floor. Biotic changes driven by such live/dead interactions have recently been termed taphonomic feedback (TF) to stress a) the role of post-mortem processes in the availability of hardparts, and b) that not only does the life assemblage influence the death assemblage, but the accumulation of a death assemblage affects the living one. This paper presents a quantitative test for the operation of taphonomic feedback in the fossil record. Assemblages from Miocene strata of Maryland exhibit a statistically significant correlation between the abundance of shell-gravel dwellers (including epifauna and infauna) and sediment shelliness consistent with faunal changes predicted by TF. Alternative explanations for the correlation, such as differential preservation potentials of soft-bottom and shell-gravel taxa, faunal response to changing water energy, and live/live interactions, can be rejected. The operation of TF has several implications for analysis of the fossil record: a) as a driving mechanism for faunal change in benthic communities; b) as an approach to reconstructing patterns in the accumulation (and non-accumulation) of hardparts and sediment; and c) as an indication of the apparently prolonged post-mortem persistence of skeletal material in some settings and the biologically and taphonomically complex origins of many densely fossiliferous deposits.*

## INTRODUCTION

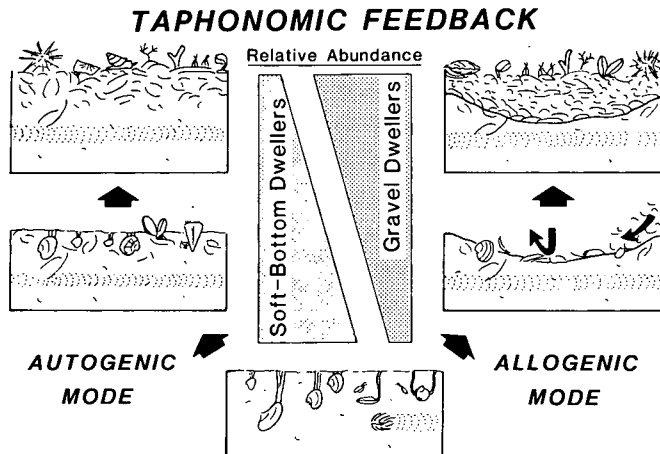
For the paleoecologist, taphonomic analysis usually focuses on how death assemblages are derived from life assemblages. Discarded hardparts, however, can change the physical characteristics of benthic habitats and thus have ecological consequences that go beyond conventional concerns of post-mortem information loss. Skeletal material provides islands of hard substrata in otherwise soft-bottom habitats and, where hardparts accumulate in abundance, transforms the sea floor into a coarser, firmer, and topographically more complex ben-

thic habitat. The development of a shell-gravel will facilitate species which require or prefer these conditions, and at the same time will inhibit successful colonization by earlier species that can tolerate only the initial soft-bottom conditions.

The accumulation of dead shell material thus has predictable consequences for the composition and dynamics of benthic communities. Kidwell and Jablonski (1983) referred to the spectrum of live/dead interactions as taphonomic feedback (TF), and suggested that TF was an important driving mechanism for ecological succession in fossil as well as recent benthic communities. TF can play a role in both autogenic and allogenic successions because the initial concentration of hardparts essential to the process can result from biotic (e.g., gregarious behavior, mass mortality in the local community) as well as abiotic processes (storm concentration of the local death assemblage, delivery of exotic benthic and nektonic planktonic hardparts) (Fig. 1).

Like most hypothesized biological processes, TF is difficult to demonstrate unambiguously in the fossil record. TF refers to the response of living benthos to the *in situ* accumulation of dead hardparts, and so the biotic interaction itself will yield an ecologically mixed death assemblage. Later gravel-dwelling taxa (which include both epifauna and infauna) occupy in large part the same sedimentary volume as the original soft-bottom community. This mixing of sequential, ecologically distinct species associations can be aggravated by physical reworking and bioturbation. Dissection of a shell-gravel deposit influenced by taphonomic feedback will thus commonly fail to reveal a microstratigraphic record of the process. An alternative strategy of testing for TF is required.

If live/dead interactions play an important role in shaping benthic ecosystems, strata containing greater densities of shell material should contain assemblages with greater relative abundances of gravel-dwelling species (Fig. 1). The test used here is to determine whether faunal composition varies significantly as a function of sediment shelliness. The null hypothesis is one of no correlation: dead hardparts did not play a role in living communities and the shell beds had ecological significance only as post-mortem records of live/live biotic interactions, shared environmental tolerances, and chance colonizations. If compo-



**FIGURE 1**—The accumulation of abundant dead shell material can change the composition of benthic communities by progressive alteration of the physical habitat. The broad range of direct and indirect influences of dead hardparts on living organisms has been termed taphonomic feedback (Kidwell and Jablonski, 1983). These live/dead interactions can mediate faunal change along two basic pathways. In the autogenic mode, the initial community responds to the accumulation of its own death assemblage, whereas in the allogenic mode, the concentration of shells reflects physical processes as well (storm reworking of dispersed shells, delivery of exotic hardparts). Because later shell-gravel-dwelling colonists occupy in large part the same sedimentary volume as earlier soft-bottom colonists, faunal changes mediated by taphonomic feedback result in ecologically mixed fossil assemblages.

sition does correlate with shell abundance, TF becomes a null hypothesis and alternative explanations must be rejected. Kidwell and Jablonski (1983) have already discussed the natural history of and experimental evidence for live/dead interactions in modern benthic ecosystems. A brief update of this review is provided here.

### TAPHONOMIC FEEDBACK AND ITS PREDICTIONS

#### Facilitative Effects of Individual Hardparts and Shell Gravels

Dead hardparts influence benthic organisms in several ways. Individual dead hardparts (like some living skeletonized organisms) are islands of hard substrata within soft-bottom habitats and provide attachment sites for sessile epifauna, especially encrusters and borers (Table 1). These provide some of the most familiar examples of what Kidwell and Jablonski (1983) referred to as facilitative taphonomic feedback, wherein the presence of dead hardparts improves the likelihood of establishment and survival of an adaptive type. This is a taphonomic analog to ecological facilitation in the sense of Connell and Slayter (1977, p. 1123), in which "later [species] can become established and grow only after earlier ones have suitably modified the conditions."

The suitability of a hardpart for colonization is influenced by its size and shape as well as its burial history (Durringer, 1985; Keough, 1984; Karlson and Cariolou, 1982; McLean, 1983). Colonization can in turn determine the hardpart's further value as a substratum (the reader is referred to Kidwell and Jablon-

ski, 1983, for further discussion and literature citations for all of these topics). For example, hermit crab colonization reduces the likelihood of shell burial and thus improves conditions for later encrusting colonists (Conover, 1975; McLean, 1983; Stachowitsch, 1979); whereas boring organisms dramatically reduce the residence time of shells on the seafloor (Driscoll, 1970; Lewy, 1981; Henderson and Styan, 1982). Such occupation of shell debris not only is one of the most commonly cited modes of facilitative TF, but represents a major evolutionary pathway by which organisms requiring hard substrata can reinvade soft substrata (Savazzi, 1982; Seilacher, 1984).

In addition to sites of attachment, individual hardparts provide domiciles and other refuges for benthic organisms (Table 1), and can govern reproductive success, thereby impinging directly on ecological replacement and species succession. Many gastropods tolerant of soft bottoms require hard attachment sites for egg capsules (Fretter and Graham, 1962), and experiments by Brenchley (1981a) suggest that the availability of such hard substrata limits reproductive output of *Ilyanassa obsoleta*. Dead shells, serving as domiciles, are often the limiting resource controlling distribution and abundance of octopods and hermit crabs (Mather, 1982a, 1982b; Fotheringham, 1980; Ambrose, 1982; Young, 1979; McLean, 1983), and the characteristics of the available dead shells can profoundly influence hermit-crab population structure. For example, in the Bay of Panama, individuals occupying shells large enough to allow growth will put effort into growth, while crabs in shells too small to permit growth allocate more time and effort to reproduction (Bertness, 1981).

Because the shells of living organisms—including infauna (Schäfer, 1972; Peterson, 1983)—can be encrusted and bored, clear evidence for post-mortem utilization of the hardparts is necessary. Colonization of shell interiors is one valuable criterion (e.g., Baluk and Radwanski's [1985] citation of *Crepidula* inside Miocene gastropod shells, and Kaiser and Voigt's [1983] discovery of fossil gastropod eggs in living chambers of Pleistocene ammonites). Sando (1984) provides a series of valuable criteria for discriminating pre- and post-mortem colonization of skeletonized epifauna.

As hardparts accumulate in abundance at a site, they increase the stability (erosion resistance) and topographic complexity of the sea floor and also alter its mass properties. The initially fine-grained, soft substratum becomes coarser grained and more firm, facilitating colonization and survival of species that require or prefer firm-bottom or shell-gravel conditions. The development of many bioherms and other biological build-ups provides good examples of autogenic and allogenic ecological successions driven largely by TF. Initial colonists utilize dispersed dead hardparts or small patches of concentrated hardparts, and through their own contribution to the death assemblage and influence on boundary-layer hydrodynamics (retardation of currents, baffling and trapping of sediment) facilitate further growth and colonization (Bosence, 1984; Lake, 1981; Narbonne and Dixon, 1984; for other examples see Kidwell and Jablonski, 1983). In the Permian of Venezuela, large sponges attached to shell debris provided attachment sites for brachiopods in an otherwise soft-bottom habitat (Hoover, 1981). As Hoover points out, in this and many other examples of shell gravels, the availability of suitable attachment

**TABLE 1**—Examples of facilitative interactions between living benthos and dead hardparts.

## ENCRUSTERS AND BORERS OF DEAD HARDPARTS

Colonist	Substratum	Age	Reference
lunulitiform bryozoa	skeletal debris	Recent	Cadee (1975)
boring sponges	skeletal debris	Recent	Young & Nelson (1985)
bryozoa	skeletal debris	Neogene	Balson & Taylor (1982)
bryozoa	erect bryozoa	Paleogene	Thomsen (1977)
sponges, thallophytes, polychaetes, phoronids	ammonites	Cretaceous	Henderson & McNamara (1985)
algae?	belemnite rostra	Cretaceous	Radwanski (1972)
thecideids, bryozoa	erect bryozoa	Jurassic	Walter & Almeras (1977)
serpulids, bryozoa, boring & encrusting bivalves	belemnite rostra	Jurassic	Holder (1972)
spirorbids, serpulids, bivalves	cephalopods	Triassic	Vossmerbäumer (1972)
thallophytes, <i>Bascomella</i>	rugose corals	Mississip.	Sando (1984)
rugose corals	skeletal debris	Devonian	Baird & Brett (1983)
tabulate corals	skeletal debris	Devonian	Brett & Cottrell (1982)
tabulate & rugose corals, bryozoa, serpulids	bivalves	Silurian	Liljedahl (1985)
algae, fungae, sponges	trilobite debris	Ordovician	Podhalanska (1984)

## SHELLS AND SHELL GRAVELS AS STRUCTURAL REFUGIA

Refugist	Structure	Refuge from	Reference
amphipods	shells, pebbles	bioturbation	DeWit & Levinton (1985)
amphipods, polychaetes, nemertean	<i>Mytilus</i> shells	physical stress	Tsuchiya (1983)
barnacles ( <i>Ibla</i> )	barnacle tests ( <i>Tetraclita</i> )	physical stress	Achituv & Klepal (1982)
<i>Littorina</i>	barnacle tests	wave shock	Underwood & McFayden (1983)
anemones	attach shell debris	dessication	Hart & Crowe (1977)
sclerosponges	coral rubble	intense sunlight	Scoffin & Henry (1984)
Paleogene foraminifera	skeletal debris	mechanical destruct.	Pozcryska & Voight (1985)
<i>Mercenaria</i>	shell gravel	crab predation	Arnold (1984)

## SHELLS AS DOMICILES

Inhabitant	Domicile	Reference
gobiid fish	shells	Breder (1950)
amphipods	shells	Carter (1982)
octopods	gastropod shells, <i>Trachycardium</i>	Mather (1982a,b)
pagurid crabs	gastropod shells	Conover (1975)
pagurid crabs	gastropod shells	Fotheringham (1980)
pagurid crabs	gastropod shells	Young (1979)
pagurid crabs	gastropod shells	McLean (1983)
Tertiary limpets ( <i>Crepidula</i> )	larger gastropod shells	Baluk & Radwanski (1984, 1985)

## SHELLS FOR ATTACHMENT AND AS A FOUNDATION FOR BIOHERM GROWTH

Colonist	Substratum	Age	Reference
brachiopods	scallop shells	Recent	Richardson (1981)
coralline algae & vermetids	skeletal debris	Recent	Bosence (1984)
deep sea limpets	squid beaks, fish bones	Recent	Marshall (1983), Hickman (1983)
sponges	skeletal debris	Permian	Hoover (1981)
microcrinoids	nautiloid body chamber	Mississip.	Mapes et al. (1986)
algae & gastropods	skeletal debris	Lower Carbonif.	Wright & Wright (1981)
lithistid sponges	crinoidal debris	Silurian	Narbonne & Dixon (1984)

sites is not reflected in the grain size of the sedimentary (non-bioclastic) matrix.

Shell-gravel conditions can facilitate many infauna as well as epifauna (Table 1). Dead shells provide attachment sites for byssate larvae and trap organic-rich mud, increasing the retention of both larvae and juveniles and providing niches for small-bodied deposit feeders (Carriker, 1956; Dauer et al., 1982). Shell debris also reduces the foraging efficiency of predators, especially crabs, thus allowing infauna to attain a size refuge from predation (Arnold, 1984; Gallagher et al., 1983; Blundon and Kennedy, 1982; Revelas, 1982).

#### Inhibitory Live/Dead Interactions

Abundant dead shells can inhibit or preclude the survival of certain species or adaptive types by restricting infaunal habitat space and by altering sediment textures. This is analogous to the ecological inhibition model of Connell and Slayter (1977, p. 1123), wherein "later species cannot grow to maturity in the presence of earlier ones."

Inhibitory biotic interactions in level-bottom settings have been far more rarely documented than facilitative interactions in similar settings. Thus, the importance of inhibitory TF in shaping and maintaining benthic communities is virtually unknown. Dauer et al. (1982) have found that total numbers of nematodes and harpacticoid copepods are always lower underneath clumps of dead oysters than in shell-free sediments, probably because porewaters underneath the oysters are anoxic. A more common factor affecting infaunal survival in shell-rich substrata, however, appears to be difficulty in penetration. Newell and Hidu (1982) found that the resistance of sediment to penetration is directly proportional to increasing particle size, and that growth rates of the infaunal bivalve *Mya* are inversely related to physical resistance. Relatively slow rates of growth have also been documented for *Mercenaria* and for *Sanguinolaria* in shell-rich sediments compared with shell-free, soft sediments (Walker and Tenore, 1984; Peterson and André, 1980), although the decrease in growth rate may be due to inhibited feeding rather than to difficulty in burrowing. Whatever its cause, the slowed growth, which delays attainment of a size refuge, increases the probability of predation among these infauna (Pearson et al., 1981; Blundon and Kennedy, 1982; Arnold, 1984). Difficulty in reburrowing into the resistant substratum also increases the probability of predation.

Mobile deposit feeders can also be expected to be inhibited by the accumulation of dead shell material in the substratum. Readjustments in the direction of movement (e.g., Levinton, 1979), lowered microbial biomass (Dale, 1974), and sorting of size-heterogeneous sediment can reduce the time and efficiency of food ingestion for larger, skeletonized taxa such as echinoids and mollusks. Resistance of the sediment to penetration should also become prohibitory with progressive shelliness of the substratum.

Infaunal clam densities are nonetheless very high in shell-rich substrata—for *Mercenaria*, they are higher than on soft substrata (Walker et al., 1980)—although body sizes are low. It thus appears that the advantageous refuge from predation that shell gravels provide infauna outweighs the disadvantages of slowed growth. A progressive increase in sediment shelliness

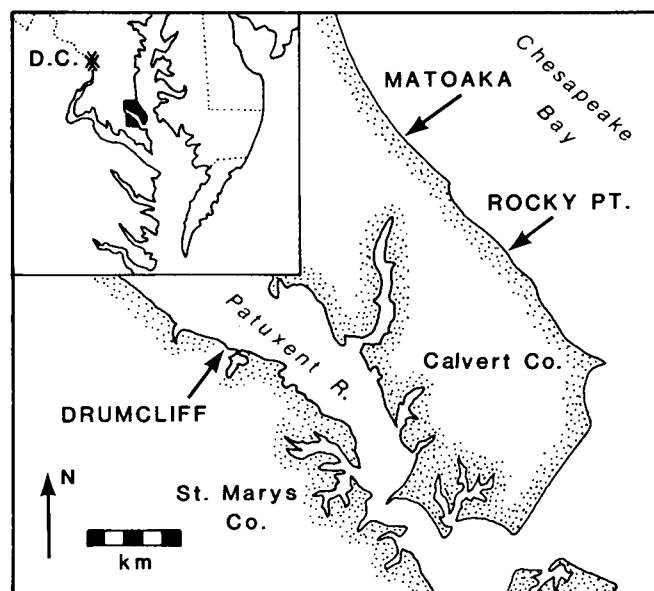


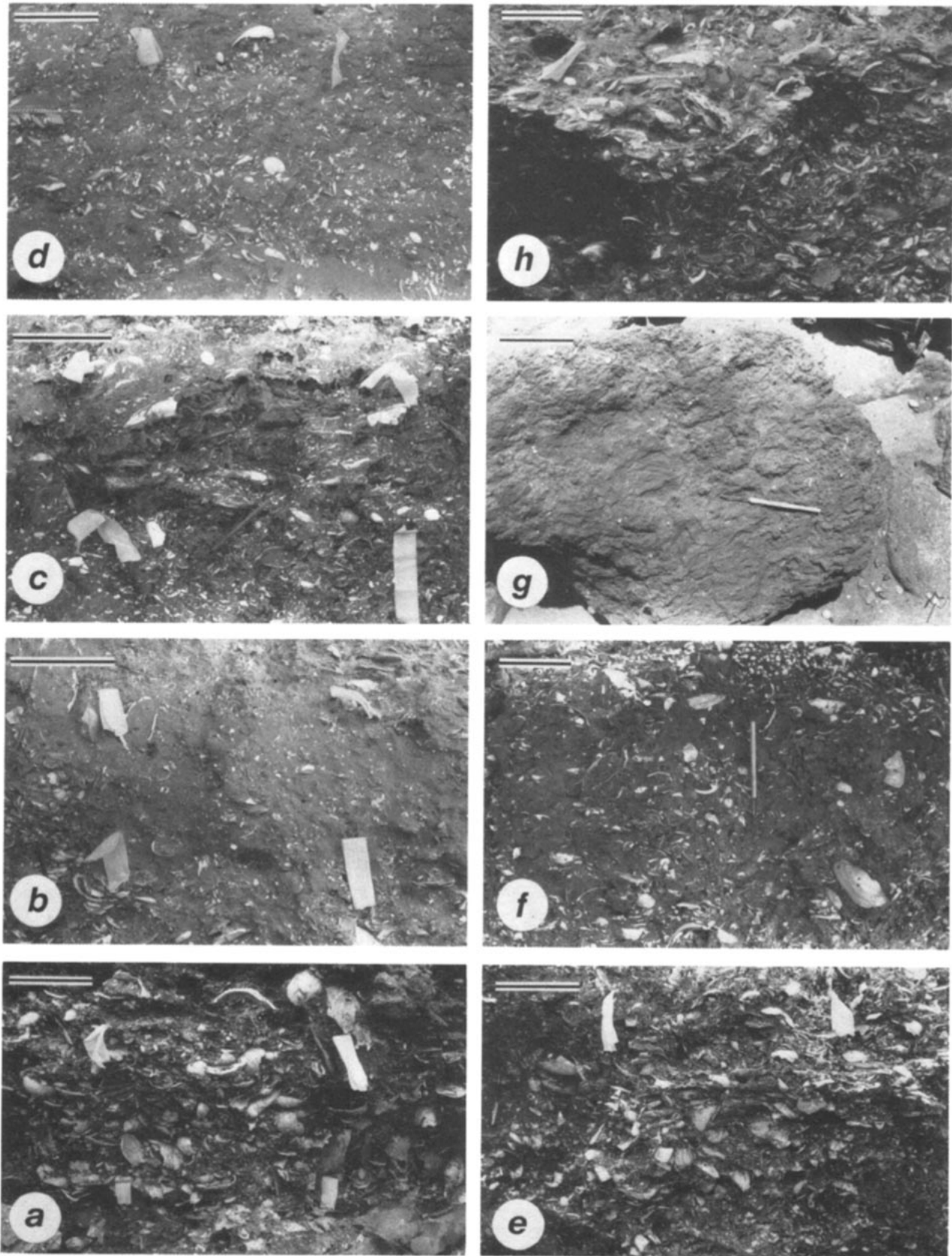
FIGURE 2—Location of sampled exposures of the Drumcliff Member, Choptank Formation (Miocene). Study area marked in black on map inset.

should, however, restrict the free movement of mobile infauna and eventually eliminate infaunal habitat space. The expected pattern is loss of mobile deposit feeders and relatively large-bodied suspension-feeding infauna, with comparative enrichment of shallow-burrowing, small-bodied infauna, nestling species, and infaunal species that can tolerate semi-infaunal positions.

#### METHODS AND STUDY AREA

The relationship between faunal composition and sediment shelliness was evaluated quantitatively at three exposures of the richly fossiliferous Drumcliff Member (Gernant, 1970) of the Middle Miocene Choptank Formation in the Maryland Coastal Plain (Fig. 2). The 2-to-10-m-thick Drumcliff Member consists of a series of shelly horizons which range in shell-packing density from highly dispersed fabrics in which individual shells "float" in matrix, to densely packed, shell-supported fabrics of whole and fragmental material (Fig. 3). The sedimentary matrix throughout is a bioturbated, quartzose fine sand, typically containing less than 5% silt and clay by weight (Kidwell, 1984).

The Drumcliff Member was selected for study for several reasons. Most importantly, this unit permitted an assessment of the relative abundances of species in beds of different shelliness but nearly identical sedimentary matrix, so that the effects of changing water depth or energy could be taken as relatively constant. Because the Drumcliff Member contains a very diverse fossil assemblage, including molluscs, irregular echinoids, cirripedes, bryozoans, corals, inarticulate brachiopods, and various worm tubes and borings, faunal trends are more robust than in deposits containing fewer species.



**FIGURE 3**—Outcrop photographs of sample horizons (in stratigraphic order) at the Drumcliff type locality (a–d), Matoaka (e–g), and Rocky Point (h). 10-cm scale bars.

**TABLE 2**—Numerical summary of relative abundance. n = number of individual specimens; % = percentage of total sample size; s = number of species.

EXPOSURE Sample Horizon	Sediment Shelliness	Soft-Bottom Fauna*			Gravel-Dwelling Fauna**			Epibiontic Fauna			Total Sample Size N	Total Species S
		% volume	n	%	s	n	%	s	n	%		
<b>DRUMCLIFF</b>												
Lower shell-rich	65–70	400	46	24	454	54	26	98	12	7	854	50
Lower shell-poor	10–15	546	63	24	321	37	25	37	4	6	867	49
Upper shell-rich	55–60	661	53	22	579	47	26	82	7	7	1240	48
Upper shell-poor	30	1112	83	27	220	17	16	8	1	3	1332	43
<b>MATOKA</b>												
Lower shell-rich	65–70	366	46	22	430	54	26	93	11	7	796	48
Lower shell-poor	15–20	1005	80	30	251	20	24	15	1	4	1256	54
Upper shell-poor	1–5	634	83	23	131	17	16	7	1	5	765	37
<b>ROCKY POINT</b>												
Upper shell-rich	50	452	54	31	382	46	25	82	10	6	834	56

\*Includes commensal taxa \*\*Includes epibiontic taxa

Inferences of life habits and substratum preference are strengthened by the large percentage of extant genera.

Sediment shelliness in each sample horizon was determined in the field using the visual estimation charts of Schäfer (1969; reprinted in Fügel, 1982) for shell percentage by volume. The relative abundances of species were determined from samples of approximately 800–1,300 specimens; the total number of species in each sample ranged from 37 to 56 (Table 2). In order to avoid bias from the disintegration of specimens during collection and transport, specimens were counted in the field using a modified bulk-sample method. A dissecting needle was used to pick through the sediment in the outcrop or in small handfuls of the bulk sediment. Specimens were identified to the species level in the field using species designations from the Maryland Geological Survey Miocene Volume (Case et al., 1904). Generic assignments of these species were updated using Moore (1969) for bivalves, Bretsky (1976) for lucinids, Abbott (1974) for gastropods, Cernohorsky (1984) for nassariids, Zullo (1984) for barnacles, and Durham (1953) for echinoids.

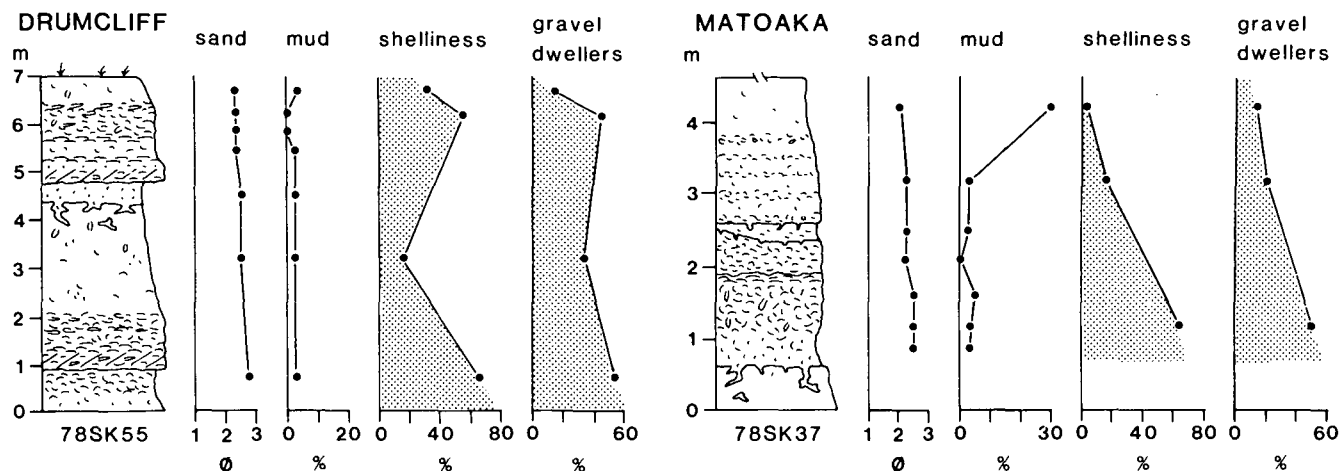
Life-habit and paleoenvironment assignments for the approximately 120 species contained in the Drumcliff samples are provided in Appendix 1. Gravel-dwelling taxa include most free-living and byssate epifaunal species, all endo- and epibiontic species, most endo-byssate species, and infaunal species belonging to genera that today prefer, or occur in greatest densities in, shell-gravel habitats, and that do not range outside of shell-gravel lithofacies in the Maryland Miocene study area.

Gravel-dwelling, infaunal bivalve taxa include the robust venerid bivalves *Mercenaria* and *Callista*, semelids, *Astarte*, large-bodied *Spisula*, *Laevicardium*, and the nestlers *Hiatella*, *Sphenia*, and "*Petricola*" (= *Pleiorytis*?). Many infauna excluded

from the gravel-dwelling category probably tolerated or actually preferred shell-gravel habitats. These include small-bodied and shallow-burrowing species capable of living in shell-gravel interstices (e.g., small, abundant species such as *Spisula subparilis* and *Lucina* [*Parvilucina*] *crenulata*; see Jones and Thompson, 1984 for ecology of modern *Parvilucina* in soft-bottom and winnowed, carbonate-rich sediments). Commensal organisms (kelliid and leptonid bivalves), which are non-diagnostic of sedimentary substrata, were grouped with soft-bottom taxa. The number of Maryland Miocene infaunal species designated here as tolerant or characteristic of shell-gravel habitats is thus probably a conservative estimate.

The relative-abundance data are based on counts of whole specimens and a few kinds of shell fragments (hinge-bearing fragments of bivalves; gastropods with apex intact or columella retaining apical end). Endobionts such as clonid sponges, the worm *Polydora*, and lithophagid bivalves were inferred from characteristic traces in shell substrata, and were counted as one individual per infested shell. Encrusting bryozoan colonies were counted in the same way.

Disarticulated barnacle plates are not included in the relative abundance calculations because of their consistently large numbers, which would have overwhelmed the remainder of the fauna statistically. There are hundreds of plates per sample (see Appendix 1), representing 10% or more of the total specimen count. Most of the disarticulated plates are very small (< 5 mm) and quite possibly allochthonous. Articulated barnacles, attachment scars, and basal plates attached to shell substrata were far less abundant than disarticulated plates (see Appendix 1). Because all barnacle data were excluded from analysis, and because other endo- and epibiontic data reflect the number of infested shells rather than the number of



**FIGURE 4**—Schematic stratigraphic columns for the Drumcliff type locality and Matoaka, with modal sand size in matrix ( $\phi$  units), % mud by weight in matrix, sediment shelliness (% volume of bulk sediment), and relative abundance of gravel-dwelling fauna (% of total specimens counted). Cross-hachured beds in the Drumcliff section are indurated sandstones. Differences in faunal composition between adjacent shell-poor and shell-rich horizons in each section are significant at the 99% level (chi-square test) and track upsection variation in sediment shelliness.

infesting individuals, frequencies of encrusters and borers are underestimated. Observed frequencies of epibiont infestation (Table 2, includes endobionts) are, by any measure, probably only minimum estimates, because of the disintegration of bored shells into unrecognizable shell fragments.

Sample horizons in each locality were selected in order to analyze a series of alternating shell-rich and shell-poor beds containing very similar sedimentary matrix. The exception is the uppermost sampled horizon at the Matoaka exposure (Fig. 4), which contains 33% mud and was sampled primarily to determine the composition of an undoubtedly soft-bottom assemblage. Shell-rich horizons in which epifaunal species were clearly very abundant or dominant were avoided in order to make the test for TF as conservative as possible. Indurated beds were also avoided in order to minimize bias from differential preservation and extractability of faunas.

## RESULTS

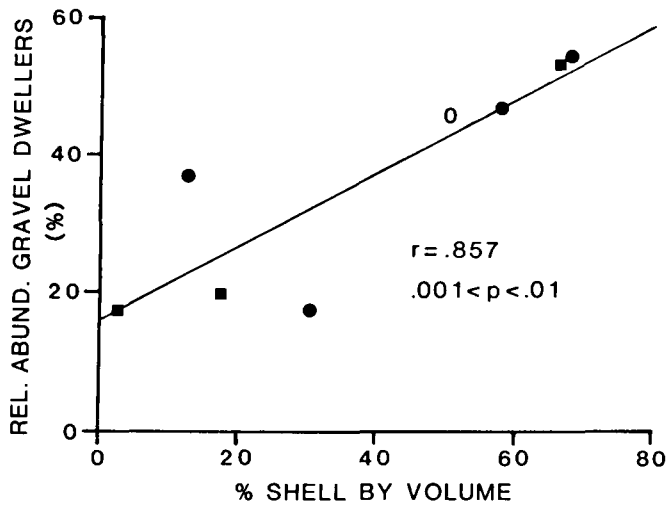
All collections exhibit the expected correlation between life habit and sediment shelliness (Fig. 4). In each exposure, shell-poor horizons were dominated by infauna preferring soft-bottom conditions, and shell-rich horizons contained a significantly higher proportion of epifauna and other taxa preferring shell-gravel habitats. The between-sample differences in the relative abundances of species within both the Drumcliff and Matoaka exposures are significant at the 99% level using a chi-square test. Tallies of the number of species (S) of each life habit do not reveal a trend (Table 2); similar numbers of soft-bottom and shell-gravel species occurred in both shell-rich and shell-poor horizons.

Upsection reversals in sediment shelliness at the Drumcliff

type locality and monotonic decline in sediment shelliness at the Matoaka exposure (Fig. 4) are accompanied by reversals in the abundance of gravel-dwelling species, but are not reflected in the texture of the quartzose sedimentary matrix or in the size-frequency distribution of shell material. The matrix throughout the Drumcliff shell bed is a clean, well-sorted, fine sand containing less than 6% mud (this excludes the upper sampled horizon at Matoaka, which actually lies stratigraphically above the Drumcliff Member s.s.). As evident from the outcrop photographs in Figure 3 and the taxonomic lists in Appendix 1, each sample horizon contains a range of shell material from large, whole specimens to small, fragmental pieces and unbroken specimens of small species.

A single horizon of shell-rich sediment (50% shell; 10% mud by weight) was sampled from the top of the Drumcliff Member at Rocky Point (Fig. 2) for comparison with the Matoaka sequence. Forty-six percent of the assemblage consisted of gravel-dwelling fauna (Table 2), which is intermediate to and significantly different from the composition of horizons having greater and lesser shelliness at Matoaka. Stratigraphically, the Rocky Point sample horizon lies between the second and third sample horizons at Matoaka, and thus permits another test of whether faunal composition tracks an upsection reversal in sediment shelliness.

Faunal relative abundance exhibits a highly significant relationship with sediment shelliness ( $r = 0.857$ , 6 d.f.,  $p < 0.01$ ; Fig. 5) when the eight sampled horizons are analyzed as a group. The correlation coefficient increases ( $r = 0.886$ ) if infaunal taxa known to occupy a wide range of substrate types (e.g., *Laevicardium*, semelids) are excluded from the class of gravel dwellers. Thus, the results appear to be robust concerning possible misassignment of gravel-preference to eurytopic infaunal species in the Miocene assemblages. Moreover, relative abundances of gravel-dwelling taxa are independent of



**FIGURE 5**—Simple linear regression of % gravel-dwelling fauna against sediment shelliness demonstrates a highly significant positive correlation consistent with the operation of taphonomic feedback. Symbols denote sample locality: black circle = Drumcliff, open circle = Rocky Point, black square = Matoaka.

both sample size (simple linear regression;  $r = 0.086$ , 6 d.f., N.S.) and species richness ( $r = 0.405$ , 6 d.f., N.S.) (Fig. 6).

**DISCUSSION**

Several alternative hypotheses to directional faunal change driven by taphonomic feedback can be advanced to explain the

observed pattern. All of these can be rejected or accommodated by the TF model.

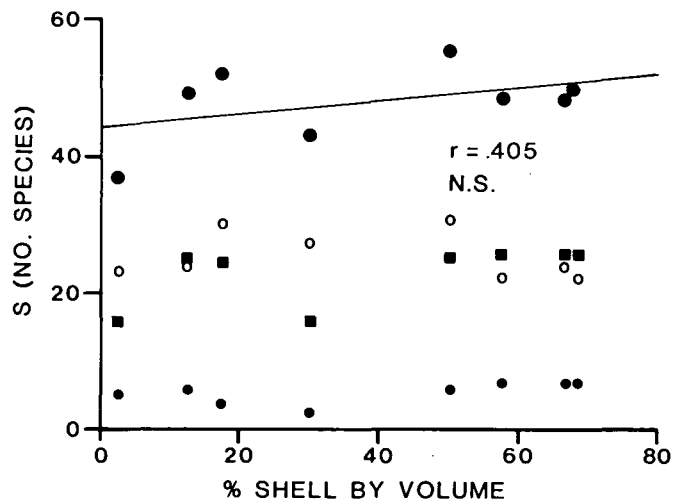
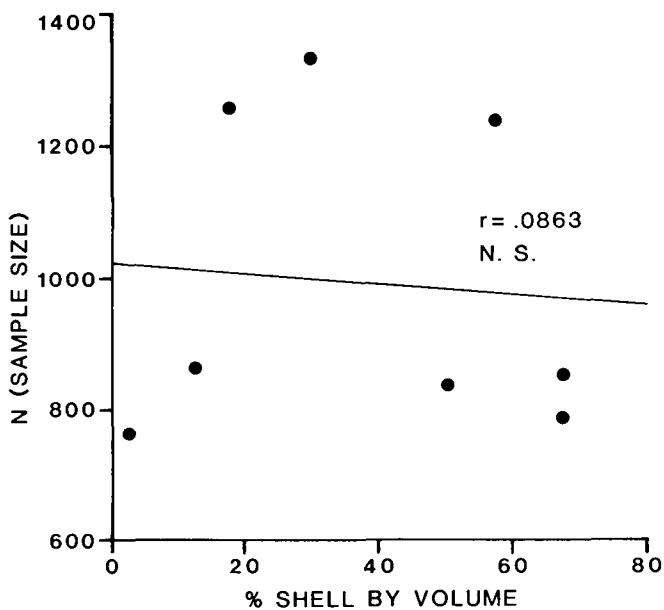
**Statistical Artifact**

The relative abundances of gravel-dwelling fauna are probably not artifacts of sample size. Total sample size  $N$  is not correlated with sediment shelliness (Fig. 6), and neither the percentage of gravel-dwelling fauna nor the species richness of gravel faunas show significant variation with sample size based on simple linear regressions.

Moreover, the relationship observed between faunal relative abundance and sediment shelliness (Fig. 5) is probably not a product of auto-correlation because the two metrics are independent. Sediment shelliness was determined by visual estimation of the volume of shell in the bulk sediment, and relative abundance is a numerical value calculated as a percentage of the total number of specimens ( $N$ ). Biomass estimates of relative abundance were not used. These incorporate a body-size factor that could be confounded with volumetric estimates of shelliness.

**Post-Mortem Mixing of Allochthonous Assemblages**

The shell-rich as well as shell-poor layers appear to be *in situ* accumulations of essentially autochthonous (parautochthonous) hardparts (Kidwell, 1982a, 1982b). Neither soft-bottom nor gravel-dwelling taxa show evidence of transport, such as strong size-sorting or preferential breakage of delicate specimens, and the fossils are not associated with appropriate high-energy sedimentary structures. Moreover, the Drumcliff Member has depositional rather than erosional contacts with laterally adjacent units, and potential source beds for allochthonous



**FIGURE 6**—Simple linear regressions of sample size ( $N$ ) and species richness ( $S$ ) plotted against sediment shelliness indicate no significant correlation. Symbols in the species richness plot: large black circles = richness of total sample; small black circles = epibionts; open circles = soft-bottom taxa including commensals; black squares = gravel-dwelling taxa, including epibionts.



hardparts (including underlying strata) are either unfossiliferous or contain taxonomically dissimilar and low-density fossil assemblages (Kidwell, 1984).

#### Selective Destruction of Soft-Bottom Fauna

Differences in faunal composition between shell-rich and shell-poor horizons could reflect preferential destruction of soft-bottom taxa during episodes of shell concentration or diagenesis, resulting in a relative enrichment of gravel-dwelling species in shell-rich horizons. Several lines of reasoning argue against this explanation.

1. Epifaunal specimens tend to have lower preservation potential than infaunal specimens because of longer exposure time on the sea floor and greater likelihood of transport (e.g., Cadée, 1968).
2. Even aragonitic taxa can have long exposure times on the sea floor. Young and Nelson (1985) refer to the low preservation potential of large aragonitic bivalves (*Glycymeris* and *Humularia*) on the Scott Shelf due to boring by sponges, and yet those bivalve specimens are approximately 1,000 years old, which is more than sufficient time to elicit taphonomic feedback. These observations, and the widespread occurrence of abundant shell debris in surficial sediments of modern shelves (McManus, 1975; Nelson, 1978; Nelson and Bornhold, 1983; Farrow et al., 1984; see Kidwell and Jablonski, 1983, for review of TF in shelfal shell gravels), suggest that the rapid rates of aragonitic shell destruction documented for some marginal marine settings (e.g. Cummins et al., 1986) do not apply to all subtidal settings.
3. The majority of shell-gravel species in the Drumcliff are aragonitic and thus should have relatively low preservation potential during post-burial diagenesis. Forty-one of the 54 gravel-dwelling species are aragonitic (half of these are bivalves), as are 39 of the 53 total epifaunal species (soft- and gravel-bottom habits; epibionts excluded) (see Appendix 1). The most common gravel-dwelling taxa in shell-rich horizons are *Chesapecten* (primarily calcitic); *Crucibulum*, *Mercenaria*, and *Laevicardium* (all aragonitic); and *Iso-gnomon* (bimineralic). *Crepidula*, *Anadara*, *Astarte*, and *Semele* (all aragonitic), and *Mytilus* and *Anomia* (both bimineralic) are the next most abundant gravel dwellers (all mineralogy determinations follow Carter, 1980, and Taylor et al., 1969, 1973). The diverse mineralogies and range of shell size and sturdiness suggest that assemblages in shell-rich horizons did not necessarily suffer greater bias from selective destruction than those in shell-poor horizons.

#### Change in Physical Environment

Physical environmental changes other than sediment shelliness do not appear to have driven the observed changes in faunal composition. Sedimentary grain-size parameters and structures are consistent among the sampled intervals of the Drumcliff Member, and thus changes in the relative abundances of species are probably not tracking changes in water energy. The one exception is the uppermost sampled horizon at Ma-toaka. Its low abundance of gravel-dwelling species probably does reflect the greater muddiness and low shell content

of the matrix. Removal of this data point from the graph in Figure 5 does not significantly reduce the correlation coefficient.

There is no indication that fluctuations in either salinity or oxygen drove changes in the composition of fossil assemblages or caused the formation of shell-rich horizons. The assemblages lack genera restricted to brackish or freshwater conditions, and euryhaline taxa such as *Caryocorbula* are distributed among samples without regard for sediment shelliness (Appendix 1). The byssate, semi-infaunal to epifaunal bivalve *Iso-gnomon*, which Fürsich (1981) suggested was euryhaline in the Jurassic, occurs in greatest abundance in shell-rich horizons in the Drumcliff Member, but does not occur in all shell-rich horizons and is also known from shell-poor strata elsewhere in the Choptank Formation (Appendix 1; Kidwell, 1982a, 1984).

#### Byproduct of Population Explosions

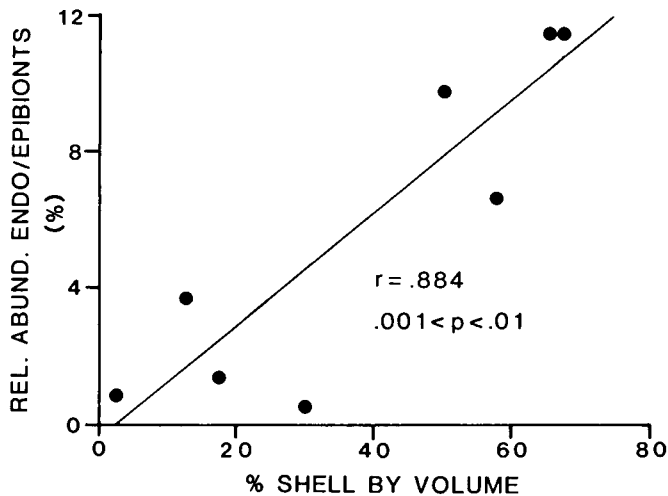
Fossil-rich horizons cannot be explained as explosions of species having high shell production rates. The major contributors to shell-rich horizons, both numerically and in terms of biomass, are not opportunistic taxa (using Levinton's [1970] criteria and by comparison with living relatives), and show evidence of long life spans (e.g., massive shells, many growth lines). The only exception is the upper, shell-poor horizon at Drumcliff. More than 40% of this sample consists of the probable opportunist *Spisula subparilis*, and probably explains why this point falls well below the regression line in Figure 5.

#### Biotically Driven Ecological Succession

The greater representation of gravel-dwelling fauna in the most densely packed shell horizons suggests a directionality that is consistent with live/dead interactions but not with live/live interactions (Kidwell and Jablonski, 1983). Live, mobile infauna are unlikely to facilitate epifauna; in fact, bioturbators are known to have an inhibitory effect on live epifauna (Rhoads, 1974; Brenchley, 1981b; Thayer, 1983). Inhibition of infauna by living epifauna, on the other hand, would require improbably high population densities before suspended food or access to the water column (or to sediment during larval settlement) became limiting. Furthermore, epizoans on infaunal shells and on the interiors of epifaunal shells not only provide evidence for live/dead interactions, but demonstrate that discarded hardparts remained near the sea floor and were thus ecologically influential in shell-rich horizons for some time after death (Fig. 7).

Taphonomic feedback can operate alone or in combination with other biotic and abiotic processes. Rejection of all alternative explanations for faunal change is therefore not a prerequisite to acceptance of a TF mechanism. For example, a shallowing phase will often result in an increase in sediment shelliness owing to more vigorous winnowing or increased delivery of exotic hardparts. The accompanying faunal change may be a response to water depth alone, but will commonly also reflect concomitant changes in the substratum, including increased skeletal debris. In such situations, TF is a contributing factor to allogenic faunal change.

Skeletal material can accumulate in the absence of physical environmental change, exemplified by the formation of shell



**FIGURE 7**—Simple linear regression of frequency of endo- and epibiont infestation (% of infested shells in sample) against sediment shelliness.

gravels on starved, deep-water sea floors. TF can thus also figure in autogenic succession through the direct and indirect response of benthos to hardparts. Seilacher et al. (1985) explained shifting relative proportions of soft-bottom and gravel-dwelling species in cyclic Jurassic sediments by such a scenario, with faunal change driven by TF during intervals of reduced mud deposition.

Most shallow-water benthic successions (including bioherm growth; see Kidwell and Jablonski, 1983, for review) probably record both autogenic and allogenic phases of faunal change mediated by TF. In the Drumcliff Member, the concentration of shell material was doubtless accelerated by episodes of sea-floor reworking, which also further mixed contributions from successive death assemblages.

#### CONCLUSIONS AND IMPLICATIONS

High proportions of gravel-dwelling taxa within shell-rich beds suggest TF but are not unique to settings in which TF has operated. Consequently, rigorous testing of TF requires additional lines of evidence by which alternative hypotheses can be rejected. In the Maryland Miocene, sedimentologic, neontologic, stratigraphic, and biostratigraphic data could be combined to rule out the reasonable alternatives.

The operation of taphonomic feedback has several positive implications for analysis of the fossil record:

1. Evidence for TF in living and fossil assemblages indicates that benthic communities are influenced by a class of interactions not generally considered by ecologists and paleoecologists (Peterson, 1983). Faunal changes mediated by TF entail different sorts of biotic interactions, with different expected outcomes, than those driven by live/live interactions (e.g., competitive exclusion, stochastic colonization) or physical environmental change. In addition, the operation of TF underscores the ecological significance of such factors as patterns of hardpart production and delivery from

other habitats, and rates of hardpart burial and destruction on the sea floor. Opportunities and pathways of TF have probably changed over the course of the Phanerozoic with the evolution and environmental expansion of hardpart producers, utilizers, and destroyers (Kidwell and Jablonski, 1983; Kidwell, 1985a; Bambach, in press).

2. The ability to identify instances of TF provides a means of recognizing patterns of fossil and sediment accumulation (e.g., Kidwell and Jablonski, 1983; Kidwell and Aigner, 1985). Because the maintenance of abundant shells at the depositional interface often involves sea-floor reworking and sediment bypassing or starvation, TF represents an additional paleontologic key to episodes of erosion and sedimentary omission in the stratigraphic record (e.g. Kidwell, 1985b).
3. By definition, detectable operation of TF indicates persistence of shells at or near the seafloor for ecologically significant periods of time, in contrast to actualistic evidence for rapid destruction of shells. The fossil record is a complex amalgam of environments that differ greatly in their destructiveness, ranging from the fleeting life spans of shells in some modern lagoons (Cummins et al., 1986) to the prolonged and eventful histories of shells in relict shelf deposits. In the Maryland Miocene, the strength of the correlation between faunal composition and shell-packing density within beds was unexpected and suggests that, the taphonomic/diagenetic filter notwithstanding, vast numbers of fossils are incorporated into the stratigraphic record, preserving an admittedly biased but surprisingly coherent signal of the original biota.
4. Shell gravels are relatively common shallow-marine lithofacies in modern and Cenozoic records, and it should be possible to trace the long-term changes in the extent of these habitats and their influence on the occurrence and interactions of marine benthos. A co-evolutionary relationship between hardpart producers and utilizers is highly unlikely, because most gravel-dwelling taxa (including endo- and epibionts) can utilize other hard substrata, such as living skeletonized hosts, cobbles, and hardgrounds. However, the extent of shell-gravel habitats has probably influenced the distribution and degree of association of sets of taxa, such that taphonomic feedback may figure in the evolutionary as well as ecological dynamics of marine benthic communities.

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## APPENDIX I

Life Habits and Faunal Abundances in the Drumcliff Member,  
Choptank Formation (Miocene), Maryland

This is a compilation of species abundances in eight sampled horizons at three localities of the Middle Miocene Drumcliff Member, Choptank Formation. Abbreviations are as follows. *Life habits*: inf dep = infaunal deposit feeder; inf susp = infaunal suspension feeder; epi byss = epibyssate (epifaunal byssally attached) suspension feeder; endo byss = endobyssate (infaunal or semi-infaunal byssally attached) suspension feeder; epib = epi- or endobiontic (encrusting or boring in shell substrata) suspension feeder; nestl susp = nestling (in cavities and gravel interstices) suspension feeder; epif plough = epifaunal plougher; epif = epifaunal unattached; inf = infaunal unattached. *Inferred substratum preference*: G = living on or within dead hardparts or hardpart-rich sediment (shell gravel); S = living on or within soft, hardpart-poor sediment; C = commensal on living organism; X = species abundance data excluded from computations of faunal composition. *References for life habits and substratum preference*: 1—Stanley, 1970; 2—Theroux and Wigley, 1983; 3—Kidwell, in prep.; 4—Abbott, 1974; 5—Coan, 1977; 6—Mauer et al., 1974; 7—Bosence, 1979; 8—Owen, 1953; 9—Moore and Lopez, 1970; 10—Walker et al., 1980; Pratt, 1953; 11—Yonge, 1951; Bahuk and Radwanski, 1979; 12—Yonge, 1946; Bassindale, 1961; Buchanan, 1958; 13—Signor, 1982; 14—Leatham and Mauer, 1975; 15—Taylor et al., 1980; 16—Brown, 1982.

	Life Habit	Refer-ence	Preferred Sub-stratum	DRUMCLIFF				MATOAKA			ROCKY PT.
				lower shell-rich	lower shell-poor	upper shell-rich	upper shell-poor	lower shell-rich	lower shell-poor	upper shell-poor	shell-rich
<b>BIVALVIA</b>											
<b>Nuculidae</b>											
<i>Nucula proxima</i> Say	inf dep	1	S	1		2	6			11	
<i>Nucula taphria</i> Dall	inf dep	1	S							1	
<i>Nucula</i> sp.	inf dep	1	S		1						2
<b>Nuculanidae</b>											
<i>Yoldia laevis</i> (Say)	inf dep	1	S	7	5		1			291	
<b>Arcidae</b>											
<i>Anadara staminea</i> (Say)	epi byss	1	G			29	62	16	22	45	22
<b>Noetiidae</b>											
<i>Striarca centenaria</i> (Say)	epi byss	1	G			8					2
<b>Mytilidae</b>											
<i>Mytilus incurvus</i> Conrad	epi byss	1	G	14	6			20	15	30	5
<i>Crenella</i> sp.	endo byss	2	G								1
<i>Modiolus ducatelli</i> Conrad	endo byss	1	S	2	12						
<b>Pinnidae</b>											
<i>Pinna harrisii</i> (Dall)	endo byss	1	S	3							
<b>Isognomonidae</b>											
<i>Isognomon maxillatus</i> (Lamarck)	endo/epibyss	1,3	G	4	6	37		13			34
<b>Pectinidae</b>											
<i>Chesapeakea nefrens</i> Ward & Blackwelder 1975	epi free	1	G	76	46	31	35	50	15	8	51
<i>Placopecten marylandicus</i> (Say)	epi free	1,2	G	1							
<b>Anomiidae</b>											
<i>Anomia</i> sp. indet.	epi byss	1,2	G			191					
<b>Lucinidae</b>											
<i>Lucina (Stewartia) anodonta</i> (Say)	inf susp	1	S			1	2		3		7
<i>Lucina (Parvilucina) crenulata</i> (Conrad)	inf susp	1,2	S	19	29	11	43	5	5	2	9
<i>Miltha (Lucinoma) contracta</i> (Say)	inf susp	1,2	S								4
<b>Ungulinidae</b>											
<i>"Diplodonta" subvexus</i> (Conrad)	inf susp	1,2	S						156		2
<b>Kellidae</b>											
<i>Aligena aequata</i> (Conrad)	epi byss	4	C	37	12	5	9	6	2	2	6
<i>Bornia mactroides</i> (Conrad)	epi byss	4	C		2					1	
<b>Leptonidae</b>											
<i>Solecardia cossmanni</i> Dall	epi byss	4	C							2	
<i>Solecardia</i> sp. indet.	epi byss	4	C	3	4						
<b>Carditidae</b>											
<i>Carditamera protracta</i> Conrad	endo byss	1,2	G					2	1		
<i>Cyclocardia granulata</i> (Say)	inf susp	1,2,5	S			1		88		3	
<b>Astartidae</b>											
<i>Astarte thisphila</i> Glenn	inf susp	1,2,6,7	G	10	5	7	11	12	50		22

## APPENDIX 1—(Continued)

	Life Habit	Refer- ence	Preferred Sub- stratum	DRUMCLIFF				MATOAKA			ROCKY PT.
				lower shell- rich	lower shell- poor	upper shell- rich	upper shell- poor	lower shell- rich	lower shell- poor	upper shell- poor	shell- rich
BIVALVIA (Continued)											
Crassatellidae											
<i>Eucrassatella turgidula</i> (Conrad)	inf susp	2,4	S	7	23	2	4	7	19		9
Cardiidae											
<i>Laevicardium laqueatum</i> (Conrad)	inf susp	1,2	G	112	100	17	29	58	54	24	73
Mactridae											
<i>Spisula delumbis?</i> (Conrad)	inf susp	1,2,6	G						3		3
<i>Spisula subparilis</i> (Conrad)	inf susp	1	S	38	21	261	565	145	86		150
Cultellidae											
<i>Ensis ensiformis</i> Conrad	inf susp	1	S							184	3
<i>Ensis directus</i> (Conrad)	inf susp	1	S				8				
<i>Ensis</i> sp. indet.	inf susp	1	S	2		4		-2	2		
Tellinidae											
<i>Tellina</i> sp.	inf dep	1,2	S	5	4		6				4
<i>Macoma lenis</i> (Conrad)	inf dep	1,2	S		1						
<i>Macoma</i> sp. indet.	inf dep	1,2	S	1							
Semelidae											
<i>Semele carinata</i> (Conrad)	inf dep	2	G	1					4		20
<i>Semele subovata</i> Say	inf dep	2	G	9	18	16	26	21			2
<i>Abra longicalla</i> (Scacchi)	inf dep	1,2	G						4		
Glossidae											
<i>Glossus fraterna</i> (Say)	inf susp	8	S	2	7	13	6	5	43		25
Veneridae											
<i>Pitar?</i> <i>subnasuta</i> (Conrad)	inf susp	1,2,6	S		2	15	64	16	11		29
<i>Callista marylandica</i> (Conrad)	inf susp	1,2	G	9				2			1
<i>Callista sayana</i> (Conrad)	inf susp	1,2	G							2	
<i>Dosinia acetabulum</i> Conrad	inf susp	1,9	S	14	2		17	21	47		10
<i>Dosinia</i> sp. (small)	inf susp	1,9	S			2	9				6
<i>Clementia inoceriformis</i> (Wagner)	inf susp	4	S								9
<i>Mercenaria mercenaria</i> (Linné)	inf susp	1,10	G	41	14			29	26		10
<i>Mercenaria cuneata</i> (Conrad)	inf susp	1,10	G		2						
<i>Mercenaria plena?</i> (Conrad)	inf susp	1,10	G	1							
<i>Mercenaria rileyi</i> (Conrad)	inf susp	1,10	G	27	25		17			1	
<i>Mercenaria</i> sp.	inf susp	1,10	G	1	3						2
Petricolidae											
" <i>Petricola</i> " <i>centenaria</i> (Conrad)	nestl susp	1,6	G	3				4	1		1
Myidae											
<i>Mya producta</i> Conrad	inf susp	1,2,6	S				2				
<i>Sphenia dubia</i> (Lea)	nestl susp	11	G		3						
Corbulidae											
<i>Corbula (Bicorbula) idonea</i> (Conrad)	inf susp	1,2	S	29	1	8	22	9	6		30
<i>C. (Caryocorbula) inaequalis</i> (Say)	inf susp	1,2	S	63	46	15	30	23	48	28	37
Hiatellidae											
<i>Hiatella arctica</i> (Linné)	nestl susp	1,2	G			9					
<i>Panopea americanus</i> Conrad	inf susp	4	S		6			2			
<i>Panopea whitfieldi</i> Dall	inf susp	4	S						17		
Pholadidae											
" <i>Martesia</i> " <i>ovalis</i> (Say)	epib	1	G			13					1
" <i>Martesia</i> " sp.	epib	1	G			3					
Pandoridae											
<i>Pandora crassidens</i> Conrad	inf susp	2	S							1	
Periplomatidae											
<i>Periploma</i> sp.	inf susp	2	S							6	
Thraciidae											
<i>Thracia</i> sp.	inf susp	2	S							2	
GASTROPODA											
Fissurellidae											
<i>Diodora nassula</i> (Conrad)	epif	4	G	3		3					
Trochidae											
<i>Calliostoma aphelium</i> Dall	epif	4	G		1	1	8	5	3		2
<i>Calliostoma philanthropus</i> (Conrad)	epif	4	G		1				1		

## APPENDIX 1—(Continued)

	Life Habit	Refer- ence	Preferred Sub- stratum	DRUMCLIFF				MATOAKA			ROCKY PT.
				lower shell- rich	lower shell- poor	upper shell- rich	upper shell- poor	lower shell- rich	lower shell- poor	upper shell- poor	shell- rich
GASTROPODA (Continued)											
<i>Calliostoma virginicum</i> (Conrad)	epif	4	G			4	2		1		4
<i>Calliostoma</i> sp. indet.	epif	4	G	6	11			5			1
Vitrinellidae (or Skeneidae)											
<i>Teinostoma liparum</i> (Lea)	epif	4	G					6			
<i>Teinostoma calvertense</i> Martin	epif	4	G				1				
Turritellidae											
<i>Turritella plebeia</i> Say	inf	12	S	275	21	39	115	22	152		56
<i>Turritella variabilis</i> Conrad	inf	12	S	25	73	212	158	47	42	34	20
Vermetidae											
" <i>Vermetus</i> " <i>graniferus</i> (Say)	epif	4	G		4		1		1		
Epitonidae											
" <i>Scala</i> " <i>marylandica</i> (Martin)	epif	4,13	G	1							
Hipponicidae											
<i>Hipponix marylandica</i> (Martin)	epif	4	G							8	
Calyptraeidae											
<i>Crucibulum costatum</i> (Say)	epif	4	G	35	32	65	15	76	26	5	31
<i>Crepidula plana</i> Say	epif	4,14	G		2	69	2	7	5		6
<i>Crepidula fornicata</i> (Linné)	epif	4,14	G						1		
<i>Crepidula</i> cf. <i>C. fornicata</i>	epif	4,14	G			1					
Naticidae											
<i>Polinices duplicatus</i> (Say)	inf	14,15	S			10		15	15		1
<i>Lunatia heros</i> (Say)	inf	14,15	S	14	26	15	24		2	11	20
<i>Sigaretus</i> (= <i>Sinum</i> ) <i>fragilis</i> Conrad	inf	14,15	S						1		
Muricidae											
<i>Echphora quadricostata</i> (Say)	epif	4,14,15	G	2	4	3	3	7	2		11
<i>Trophon chesapeakeanus</i> ? Martin	epif	4,14,15	G			4					
Coralliophilidae											
" <i>Coralliophila</i> " sp.	epif	4	G			1			1	1	
Buccinidae											
" <i>Siphonalia</i> " <i>devexa</i> (Conrad)	epif		S		2					1	1
" <i>Siphonalia</i> " sp.	epif		S								3
" <i>Buccinofusus</i> " cf. <i>B. parilis</i> Conrad	epif		S						3		
Columbellidae											
<i>Columbella</i> ? <i>communis</i> (Conrad)	epif	4,14	G					3			
Nassariidae											
<i>Nassarius</i> cf. <i>N. marylandica</i> (Martin)	epif plough	14	S			31		3	1		
<i>Nassarius peralta</i> (Conrad)	epif plough	14	S					7		13	6
<i>Nassarius</i> sp.	epif plough	14	S				4		2		
<i>Bulliopsis</i> sp.	inf	13,16	S						1		
Melongenidae											
<i>Busycon</i> cf. <i>B. coronatum</i> (Conrad)	epif	14	S					1		1	
Volutidae											
volutid sp.	epif		S				2	3		1	1
Marginellidae											
<i>Marginella minuta</i> Pfeiffer		10	S				1		1		
Olividae											
<i>Oliva litterata</i> Lamarck	epif plough	4	S	1							
<i>Olivella harrisi</i> cf. Martin	epif plough	4	S			2					
Cancellariidae											
<i>Cancellaria</i> sp.	epif	4	S						1		
Terebridae											
<i>Terebra curvilineata</i> ? Dall	inf	13	S				4				2
" <i>Terebra</i> " <i>inornata</i> (Whitfield)	inf	13	S						2	1	3
" <i>Terebra</i> " cf. <i>T. simplex</i> Conrad	inf	13	S			8	1				
<i>Terebra</i> sp.	inf	13	S	1				4			
Turridae											
" <i>Drillia</i> " <i>limatula</i> (Conrad)	epif	15	S						1		
" <i>Drillia</i> " cf. <i>D. limatula</i>	epif	15	S				2				1
<i>Pleurotoma albida</i> Perry	epif	15	S						1		
<i>Turrid</i> sp.	epif	15	S		1		1				



## APPENDIX 1—(Continued)

	Life Habit	Refer- ence	Preferred Sub- stratum	DRUMCLIFF				MATOAKA			ROCKY PT.
				lower shell- rich	lower shell- poor	upper shell- rich	upper shell- poor	lower shell- rich	lower shell- poor	upper shell- poor	shell- rich
SCAPHOPODA											
<i>Cadulus newtonensis</i> Meyer & Aldrich	inf		S	38	42	3	3	4	2	23	
POLYPLACHOPHORA											
<i>Chaetopleura apiculata?</i> (Say)	epif		G	1							
CIRRIPEDIA											
<i>Concavus chesapeakeensis</i> Zullo	epib		G,X	248 + 8 art.	193 + 5 art.	148 + 2 art.	151 + 12 art.	290 + 2 art.	168 + 1 art.	29	265 + 2 art.
DECAPODA											
crab cheliped	epif		X	1	2		1		1	1	1
ECHINOIDEA											
<i>Abertella alberti</i> (Conrad)	epif		S	5				4			2
regular echinoid spine	epif		G			1					
CHEILOSTOMATA BRYOZOA											
" <i>Membranipora</i> " spp.	epib		G	14	3	2	3	1	1	2	
" <i>Retepora</i> " spp.	epib		G	4				1			
INARTICULATA BRACHIOPODA											
<i>Discinisca lugubris</i> (Conrad)	epif		G	14	3	1	4	15	9	3	4
ANTHOZOA											
<i>Astrhelia palmata</i> (Goldfuss)	epib		G					2			1
<i>Astrhelia</i> sp.	epib		G	7	5						
PISCES											
fish scale			X							9	
ICHNOFOSSILS (SHELL SUBSTRATA)											
<i>Entobia</i> sp. (large galleries)	epib		G	41	13	33	3	29	10	2	39
<i>Entobia</i> sp. (small galleries)	epib		G	27	12	2	2	49	3	1	25
traces of <i>Polydora</i>	epib		G	4	2	7		9	1	1	2
boring barnacles?	epib		G					2			
martesiinid borings	epib		G	1	2	22				1	14