Chapter 5
Taphonomic Feedback
Ecological Consequences of Shell Accumulation

SUSAN M. KIDWELL and DAVID JABLONSKI

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1. Introduction

Sequential changes in benthic community composition have frequently been attributed by marine ecologists and paleontologists to autogenic ecologic succession in the classical sense: a biotically driven process leading to the establishment of a stable climax or mature community (Margalef, 1968; Odum, 1969). In recent years, however, the concepts of deterministic autogenic succession have been modified and supplemented by a
greater recognition of the roles of stochastic colonization and of biogenic and physical disturbance in structuring ecological communities in time and space (Colinvaux, 1973; Drury and Nisbet, 1973; Sutherland, 1974, 1981; Horn, 1974, 1976; Connell and Slayter, 1977; Connell, 1978; Lubchenco, 1978; Sousa, 1979a, 1980; White, 1979; Paine and Levin, 1981). Paleontologists have also begun to adopt a more critical approach, recognizing the many processes, both biotic and abiotic, that serve as driving mechanisms for sequential faunal changes.

One such mechanism involves the response of living organisms to the presence of dead hardparts in benthic habitats. We classify all live–dead interactions, whether facilitative or inhibitory in their effects on living organisms, as taphonomic feedback. We use the term taphonomic to emphasize the postmortem processes that figure in the availability of dead hardparts, and the term feedback to emphasize that not only does the life assemblage influence the death assemblage (as in conventional taphonomy) but the death assemblage in turn affects the life assemblage. Taphonomic feedback can figure in both autogenic and allogenic changes in community composition, because the initial accumulation of shells essential to the process can result from either biological (mass mortality, gregarious behavior) or physical processes (delivery of allochthonous hardparts, seafloor reworking, sedimentary omission).

In this chapter we review Recent and paleontologic evidence for taphonomic feedback, including new observations from Miocene shell beds in which a variety of live–dead interactions are inferred. We also discuss expected patterns in the accumulation of hardparts in the stratigraphic record, and their probable consequences for taphonomic feedback in benthic communities.

2. Recent and Fossil Examples of Taphonomic Feedback

We recognize two modes of taphonomic feedback in Recent and ancient benthic communities. First, dead hardparts of earlier species or adaptive types facilitate the establishment and survival of later species or adaptive types. For example, dead shells at or near the sediment–water interface provide hard substrata for larval and adult attachment and stabilize the substratum for firm-sediment dwellers. 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.”

Second, where buried in abundance, dead shells inhibit or preclude the survival of certain species or adaptive types by restricting infaunal habitat space and/or 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.”

2.1. Taphonomic Facilitation

2.1.1. Epizoan Communities

The most familiar example of taphonomic feedback, although it has not been discussed previously in such terms, is the development of epizoan communities on dead shells. Although epizoans on live hosts have received more attention among marine ecologists, dead shells exposed on the seafloor can also provide islands of hard substrata for epizoan colonization in otherwise soft-bottom settings. Driscoll (1967) and Driscoll and Brandon (1973), for example, have observed that an increase in benthic shelliness is accompanied by an increase in the relative abundance and diversity of epizoans in Buzzards Bay, Massachusetts; a similar relationship was observed by Eggleston (1972) in the bryozoan-rich Irish Sea. This effect has recently been verified by Dauer et al. (1982) who introduced clumps of dead oyster shells into soft-bottom communities in Lower Chesapeake Bay. They observed a significant increase in benthic macrofaunal diversity and densities, principally among mobile and sessile hard-substratum taxa. Increased abundance of certain taxa also present in the soft-bottom community was attributed to the role of the dead shells as refuges from predation.

Small hard substrata such as individual shells can have a disproportionate impact on the species richness of epizoans within benthic communities, apparently because they provide a refuge for opportunists and poor competitors. There are at least three reasons for this situation:

1. Only a small sample of the biota can settle on a small substratum, decreasing the probability that a superior competitor will be among the settlers (Jackson, 1977a).
2. It is easier for an encruster to overgrow a small surface before a superior competitor settles on it (Jackson, 1977a).
3. Shells are easily overturned by biological and physical disturbances, degrading overgrowth sequences and opening up new space for subdominants, although a very high rate of disturbance will exclude all but opportunists (Sears and Wilce, 1975; Osman, 1977; Lubchenco, 1978; Sousa, 1979b).

Observations on Recent epizoan faunas underscore the qualitative differences between live and dead shells as substrata. Many authors have
Taphonomic feedback also operates within epibiotic communities themselves. Early colonists facilitate (or inhibit) later colonists not only through biochemical and other biotic interactions (see Jackson, 1977b; Buss, 1979; Woodin and Jackson, 1979, for reviews), but also by their physical attributes. Dean (1981) found that artificial epizoan communities, including plastic vial caps simulating dead barnacle tests, significantly increased settlement of certain fouling organisms on experimental substrata near Delaware Bay (see also Reimer, 1976; Russ, 1980; Achittur and Kletal, 1982). These effects can be explained by the rugophilic settling behavior exhibited by marine invertebrate larvae, probably an adaptation for avoidance of turbulence and predators (see Crisp, 1976; Vance, 1978), and by larval avoidance of substrates already supporting superior competitors (Grosberg, 1981). In some Littorina species, population densities have also been shown experimentally to be directly related to the availability of topographic irregularities; empty barnacle tests, for example, serve as an important refuge for juveniles (Emson and Fuller-Fritsch, 1976; Raffaelli, 1978; Raffaelli and Hughes, 1978). The presence and density of unoccupied hardparts as well as living hosts can thus have a significant impact on the development and composition of epizoan communities.

Dead shells also serve as substrate for boring organisms, or endobionts. A wide variety of organisms including algae, fungi, bryozoans, sipunculids, phoronids, polychaetes, bivalves, cirtipeds, and sponges bore into calcium carbonate substrata. All of these groups have been found within fossil shells, and in many examples inferred to have been at work after death of the host (Boekschooten, 1966; Carriker et al., 1969; Bromley, 1970; Golubic et al., 1975; Voigt, 1975; Warme, 1975; Rodriguez and Gutschick, 1977; Kobuk and Kahle, 1978; Pohowsky, 1978).

As with epibionts, the survival of endobionts in soft-bottom environments is dependent on the quantity of hard substrata and their persistence on the seafloor. Although long periods of shell exposure on the seafloor result in rich endobiont infestation in the short term, the activities of these organisms in some instances eventually result in a reduction in the abundance of coarse shell material and destruction of the habitat. For example, Driscoll (1970) documents weight loss rates of up to 16% per year in bivalve shells over a 3-year period of submersion in Buzzards Bay due to endobiont infestation and, to an unknown but probably less significant extent, chemical dissolution. While the boring sponge Cliona celata is

inferred that host feeding activities benefit epizoans by channeling food-laden water (e.g., Ager, 1961; Thayer, 1974). Also, many live hosts act to maintain a constant position relative to the sediment–water interface, protecting their epizoans from sediment burial. A dramatic illustration is found in Lithophaga lessepsiana, which bores into a live-free scleractinian coral on soft bottoms associated with the Tulear reef complex southwest of Madagascar (Arnaud and Thomassin, 1976; see also Savazzi, 1982, for a probable late Eocene example of a similar association). Growth of the bivalve eventually kills its host, but once the coral is dead it no longer fends off encrusting calcareous algae or maintains its position at the unstable sediment–water interface, and the Lithophaga soon dies. Epibionts on hermit crab shells may also benefit from the ability of the living host to maintain an epifaunal life position (Conover, 1975, 1979; Stachowitsch, 1977, 1979). On the other hand, dead shells lack behavioral and structural antifouling mechanisms, such as allelopathic secretions or periostracal structures (see Jackson, 1977b; Bottjer and Carter, 1980; Bottjer, 1981, 1982a). In addition, through transport or exhumation after death, they can provide substrata in environments where potential live shelled hosts are deeply infaunal or as with cephalopods pelagic.

Some of the best-known epizoan communities in the fossil record appear to have developed on living hosts. For example, epizoans exhibit multiple generations, a fairly well-defined colonization sequence, and concentric arrays suggesting colonization on a growing substratum on particularly large, long-lived inoceramid species of the Late Cretaceous (Hattin, in press; Kauffman, 1974; see review in Jablonski and Bottjer, this volume). Although distinguishing between epizoan growth on living and dead substrata is often difficult, by examining interior surfaces of shells Hattin (in press) was able to demonstrate that in some instances dead inoceramids continued to provide habitats for a diverse epizoan association of oysters, barnacles, serpulids, and sponges.

Similarly, epizoans most frequently settled on living specimens of the Middle Devonian brachiopod Peraspirifer bownockeri, according to Sparks et al. (1980). They were also able to find examples in which the encrusting bryozoans had overgrown the commissures or hinges of their substrata, indicating that the host was dead. Other well-established examples of epizoans on dead shells include: pycnodont oysters on belemnite rostra in Cretaceous chalks of Poland (Pugaczewska, 1965), France (Jarvis, 1980), and the Western Interior (Hattin, in press); lithophagid bivalves, bryozoans, serpulid polychaetes, and clionid sponges on Late Cretaceous Pycnodonte (Bottjer, 1982b); bryozoans and other encrusters on the Jurassic limid bivalve Plagiostoma (Taylor, 1979); Ordovician edrioasteroids and encrusting bryozoans on overturned (?) strophomenid brachiopods and molluscan internal molds (Waddington, 1980; see also
the primary infesting agent in Buzzards Bay, other organisms are also known to reduce or eliminate settlement sites for future generations of epi- and endobiotic species (e.g., Driscoll, 1967; Perkins and Halsey, 1971; and references cited above).

Finally, dead shells can be important not only for adult survival but for successful reproduction. For example, many gastropods tolerant of soft bottoms require hard substrata for attachment of egg capsules (Freter and Graham, 1962; Amio, 1963). Brenchley’s (1981a) experiments suggest that availability of such hard substrata limits reproductive output of the mud snail *Ilyanassa obsoleta* in Barnstable Harbor, Massachusetts.

### 2.1.2. Shell Gravels

When present in abundance, dead shells contribute to the success of organisms other than attached epi- and endobiotic species by altering the physical properties of the bulk sediment. For example, localized patches of shell gravel on the southern New Zealand shelf provide substrata for bryozoan mounds built chiefly by *Cinctopora elegans* (Willan, 1981). These mounds, which can grow to 15 cm high and occupy an area of up to 0.5 m², support at least 26 species of epizoans from nestlers and borers to encrusters that further enlarge and stabilize the structure. Small carbonate buildups on shallow-water soft substrata can form in similar ways. Sheppard (1981) found that dead colonies of free-living fungiid corals provide substrata for a wide range of attached species on soft, lagoonal sediments in the Chagos Archipelago. This process along with introduction of live and dead skeletal debris from the reef slope appears to be capable of extending a hard substratum across the lagoon floor, permitting the establishment and sequential compositional changes of the coral reef-building community (see also Highsmith et al., 1980; Sheppard, 1982; Highsmith, 1982, and references therein).

Similar processes operate on a larger scale in the development of deep-water ahermatypic coral buildups. There, early coral colonies established on skeletal debris trap sediment and provide additional debris that serves both as substratum and stabilizing agent for a diverse coral bank fauna (Squires, 1964; Neumann et al., 1977; Wilson, 1979; Mullins et al., 1981) (Fig. 1). As Mullins et al. (1981, p. 1006) point out, the larger the structure, the greater its effect on the bottom waters flowing around it—and, we would add, the greater its skeletal production rate caused by facilitative feedback.

Walkers and Alberstadt (1975) and Walker and Parker (1976) suggest that similar feedback processes operated in ancient communities. They found that certain strophomenid brachiopods, apparently adapted for life on soft mud bottoms, preceded and contributed settlement sites for encrusting and barnacle bryozoans and other epifaunal organisms in Ordovician rocks of Tennessee. Dead shell material derived from these species provided additional attachment sites and served to stabilize the substratum, enlarging the shell patches and allowing colonization by still more epifaunal species. The authors’ interpretation of these faunal changes in terms of classical autogenic succession is discussed in Section 2.1.3. Similar faunal replacements have been described from elsewhere in the stratigraphic record (Table 1), and some workers have followed Walker and Alberstadt (1975) in directly applying the concept of autogenic succession to the observed changes.

Shelly patches coalesce into more continuous and widespread shell gravels whenever dead shell input outstrips the dilution or burial capability of finer sediments. This transformation of the seafloor into a coarse
<table>
<thead>
<tr>
<th>Age</th>
<th>Substratum-providers/stabilizer</th>
<th>Organisms</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle Ordovician</td>
<td>Orthotretacean brachiopods</td>
<td>Pentameran or stricklandian brachiopods</td>
<td>Johnson (1977)</td>
</tr>
<tr>
<td>Late Ordovician</td>
<td>Orthida brachiopods&lt;br&gt;Zygospirid and strophomenid brachiopod&lt;br&gt;Strophomenid brachiopods</td>
<td>Crinoids and bryozaans&lt;br&gt;Stromatoporoid-coral bioherms</td>
<td>Harris and Martin (1979)&lt;br&gt;Copper and Grawbarger (1978)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Diverse brachiopod-mollusc-bryozoan community</td>
<td>Richards (1972)</td>
</tr>
<tr>
<td>Middle Silurian</td>
<td>Crinoid gravel</td>
<td>Stromatoporoid and tabulate coral bioherms</td>
<td>Riding (1981)</td>
</tr>
<tr>
<td></td>
<td>Crinoidal sand</td>
<td>Crinoid and/or coral-stromatoporoid buildsups</td>
<td>Scoffin (1971), Abbott (1976)</td>
</tr>
<tr>
<td></td>
<td>Crinoidal sand</td>
<td>Stromatoporoid reef</td>
<td>Crowley (1973)</td>
</tr>
<tr>
<td></td>
<td>Crinoid calyces</td>
<td>Bryozoans, tabulate corals, inarticulate brachiopods, worms, echinoderms</td>
<td>Liddell and Brett (1982)</td>
</tr>
<tr>
<td>Early Devonian</td>
<td>Crinoid calcarenite, stabilized by massive favositids</td>
<td>Coral-stromatoporoid buildup</td>
<td>Isaacson and Curran (1981)</td>
</tr>
<tr>
<td>Middle Devonian</td>
<td>Crinoid calcarenite&lt;br&gt;Spiriferid brachiopods</td>
<td>Tabulate coral patch reef&lt;br&gt;Brachiopod clusters</td>
<td>Williams (1980)&lt;br&gt;Bray (1972), Fleiss and Bray (1977)&lt;br&gt;Snyder (1980)</td>
</tr>
<tr>
<td>Mississippian</td>
<td>Massive dendroid and encrusting bryozaans</td>
<td>Pinnate, reticulate, and sheet bryozaans</td>
<td></td>
</tr>
<tr>
<td>Late Triassic</td>
<td>Brachiopod-bivalve coquina</td>
<td>Scleractinian corals</td>
<td>Hagedorn (1978)&lt;br&gt;Hofiasz and Racki (1980), Dzulyriski and Kubicz (1975)</td>
</tr>
<tr>
<td>Late Jurassic</td>
<td>Bivalve coquinas</td>
<td>Crinoid bioherms</td>
<td>Scott and Brenckle (1977), Scott (1981)</td>
</tr>
<tr>
<td>Late Cretaceous</td>
<td>Coarse molluscan bioclastic debris</td>
<td>Radist patch reefs</td>
<td>Frost (1977, 1981) and references therein</td>
</tr>
<tr>
<td>Pleistocene</td>
<td>Sediment-tolerant coral species</td>
<td></td>
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</tbody>
</table>

*In each instance, one set of organisms exploits a substratum provided or stabilized by a different set, or encompasses a broader spectrum of taxa than the substratem producers/stabilizers.*
substratum by the in situ production of shell material can occur in any number of hydrographic settings (see Section 3), and is accompanied by epifaunal or shallow-infaunal suspension-feeders tolerant of such sediments. For example, Bosence (1979) documents a diverse Clean Algal Gravel Community in Mannin Bay, Ireland, dominated by vagile epifauna and the nonsiphonate suspension-feeding bivalve *Astarte triangularis*. In contrast, the nearby Mud Community is relatively poor in species and individuals and contains only taxa tolerant of fine sediments. Similar coralline algal gravel faunas are known from Galway Bay (Keegan, 1974) and Brittany (Cabocho, 1968). The *Lithothamnion* calcarenites of the Middle Miocene of central Poland may be an ancient analog of these deposits (Baluk and Radwinski, 1977).

Epifaunal suspension-feeding communities dominated by bryozoans are maintained on skeletal sands and gravels found extensively off the southern coast of Australia where nutrient upwelling, low terrigenous sediment supply, and sediment winnowing enhance skeletal production and minimize the rate of shell burial (Conolly and Von der Borch, 1967; Wass et al., 1970; Davies, 1979; Marshall and Davies, 1979). Similar bryozoan assemblages occur off both the southern and western coasts of New Zealand (Probert et al., 1979; Nelson et al., 1982), where ancient analogs extend at least as far back as the Oligocene (Carter, 1975; Nelson, 1978a,b). Relict shelly sediments also provide coarse, unconsolidated substrata for epifaunal and infaunal suspension-feeders on the current-swept, rocky Scottish shelf and Rockall Bank in the northeast Atlantic (Farrow et al., 1978; Scoffin et al., 1980).

Certain taxa are typically associated with sites of dead shell accumulation (e.g., Wharton and Miller, 1968, pp. 570–580). Modern glycicerid bivalves are well-known inhabitants of shelly sands and shell gravels in the English Channel (Holme, 1961, 1966) and have been described from the skeletal sands and gravels around the Florida Keys as well (Thomas, 1975). *Glycymeris* is also abundant in ancient shell-rich sediments—for example, the Eocene Gosport Sand of Alabama (Gardner, 1957); the Miocene Calvert Formation of Maryland (Thomas, 1975; Kiddwell, 1982b); and the Pliocene Yorktown Formation (Johnson, 1968; Ward and Blackwelder, 1980). Many large species of scallops also prefer shelly substrata—for example, the modern Argopecten gibbus, *Pecten maximus*, *Chlamys islandicus* and other species (Baird, 1966; Porter and Wolfe, 1971; Beu, 1978), and fossil species of *Chesapeake* (Johnson, 1968; Kiddwell, 1982b).

### 2.1.3. Taphonomic Feedback and Ecologic Succession

In reviewing the evidence for facilitative taphonomic feedback, we remain unconvinced of the purely autogenic nature of many proposed examples of ecologic succession in the fossil record. In the much-discussed Ordovician brachiopod pavements of Walker and Alberstadt (1975) and Walker and Parker (1976), for example, a clear demonstration of autogenic succession is not possible. Strophomenids served as substrata for epifaunal development only where they occur in dense bedding plane accumulations, and the succession coincides with a lithologic change from terrigenous shale to limestone. It is thus difficult to reject an alternative scenario founded on a cessation of terrigenous sedimentation followed by the accumulation of shells through attritional mortality or storm reworking (e.g., Kreisa, 1981), either of which would have produced a substratum favoring colonization by shell gravel taxa. Aigner (1982a), in fact, describes epizoan colonization of very similar Triassic shell pavements formed by storm events.

Harland (1981) makes a somewhat better case for autogenic ecologic succession in the establishment and development of Middle Ordovician coral–stromatoporoid buildups in Norway that start on an irregular seafloor containing lenses of pelmatozoan-rich calcarenite. He argues that vertical faunal changes observed within individual buildups are not the result of some physical environmental change because of the unchanging nature of the level-bottom sediments surrounding the buildups.

Copper and Grawbarger (1978) postulate interactions between physical and biotic factors in Late Ordovician buildups that start with assemblages inhabiting muddy level-bottoms and culminate in the development of stromatoporoid–coral biostromes. They found that faunal changes were controlled primarily by shallowing waters and increased turbulence, but concluded that the composition of the fauna at each stage was influenced by biological factors as well. These included the “modification of the substrate by the presence of shelly and coralline debris” (which we would regard as taphonomic feedback, possibly engendered by turbulence) as well as the “modification of currents by upright filter feeders.” Williams (1980) presents a similar picture for the development of Devonian patch reefs, while a stronger emphasis on the role of physical environmental changes in the development of Paleozoic banks and reefs is made by Hoffman and Narkiewicz (1977).

Wilson (1982) found that unstable carbonate mud and sand bottoms in the Upper Carboniferous of southern Nevada were typically dominated by endobystate bivalves and strophomenid brachiopods, but there were also more diverse patches dominated by ramose bryozoans, compositid brachiopods, and various epizoans. These patches were initiated by strophomenids that provided attachment sites for other organisms, but were enlarged by skeletal debris from in situ mortality and by current baffling of transported materials. Unlike most paleontological examples in which an increase in diversity is emphasized as evidence for autogenic succession, Wilson (1982) reports that all of the species found in later stages of
patch development were present in the initial stages—only their relative abundances changed through a combination of biologic and hydraulic shell input to the patches.

As a final example, Isaacson and Curran (1981) recognized a complex picture of successional changes in an Early Devonian patch reef by attempting to discern sequential autogenic and allogenic stages. They viewed Stage I (initial colonization and stabilization) as essentially allogenic, because the crinoid skeletal calcarenite that served as a substratum for colonizing favositid corals formed by physical sedimentary processes. Development of the reef was then largely autogenic until growth reached mean wave base, when turbulence began to play an important part in determining the composition of the reef fauna. As in this example, many proposed instances of autogenic succession in the fossil record would probably be more appropriately considered as the result of both physical and biotic factors, rather than biotic factors alone. We therefore suggest that the rubric of succession be applied with caution.

2.2. Taphonomic Inhibition

While the accumulation of dead shells creates a favorable habitat for some species, other species are put at an increasing disadvantage. Relatively little is known about the negative effects of dead shells in marine communities, and we present some ideas and examples here in hopes of stimulating further study.

As the shell content of a substratum increases, the physical properties of the sediment and the infaunal habitat are progressively altered. Dense concentrations of shell material produce a tight sedimentary fabric due to interlocking of particles having a wide size range, increasing the force required for penetration and locomotion within the substratum. High shell densities will interfere with the movements of infauna in a manner similar to that reported by Brenchley (1982) for seagrass roots and polychaete tubes, which significantly increase burial time and decrease mobility within the sediment for a variety of shelled and soft-bodied infaunal taxa (see also Peterson, 1982). Because of the unfavorableness of coarser, more resistant sediments to species adapted to sorting or ingestion of small particles in soft muds (e.g., Rhoads, 1974; Gray, 1981; Taghon, 1982; Ju-mars et al., 1972), deposit-feeding taxa in particular will decline in abundance and diversity as the shell: sediment ratio increases.

Space itself is potentially a limiting factor in marine benthic communities, so that restriction of infaunal habitat space can be responsible for changes in community composition. Much of the evidence of space-limitation is circumstantial, e.g., observations on depth stratification of suspension-feeding or surface deposit-feeding organisms within sediments (Levinton and Bambach, 1975; Levinton, 1977, 1979a; Peterson, 1979, 1980; Whitley, 1980), or apparent exclusion of mobile taxa by sedentary, sediment-binding organisms [see Woodin and Jackson (1979), Brenchley (1982), and Peterson (1982) and, for rocky substrata, Suchanek (1981)].

Experiments by Peterson and Andre (1980) provide insight into the inhibitory effects of dead shell on infauna. As part of a series of controlled experiments on suspension-feeding bivalves living in muddy sands of Mugu Lagoon, California, they found that the presence of dead shells of Tresus nuttallii and Saxidomus nuttallii significantly decreased growth rates in living populations of a third deep-burrowing suspension-feeding bivalve, Sanguinoloria nuttallii. They hypothesized that this growth reduction resulted from a cessation of feeding activity while the living bivalve repositioned itself after encountering another shell. This particular feeding behavior has been documented in the deposit-feeding gastropod Hydrobia ventrosa (Levinton, 1979b).

Peterson and Andre’s (1980) observations show that exclusion of infauna by the in situ accumulation of dead shells probably occurs for many species well before sediments become pure shell gravels. For example, when organisms such as Sanguinoloria are hindered in attaining normal adult sizes, they might remain below a body-size refuge from predation or physical disturbance, and thus be vulnerable to local extinction. Because dead shell material can hinder growth or locomotion of living infauna, these adverse effects can be felt in communities in which predation or physical disturbance maintain standing crops below those actually required for spatial competition (live–live interactions) to be important (see Peterson, 1979; Dayton and Oliver, 1980). For example, Doering (1982) demonstrated that infaunal Mercenaria that were prevented from burrowing to escape depth (by experimental reduction of amount of available sediment) had significantly higher mortality due to sea star predation.

Species expected to persist under conditions of increasing shelliness are those that can adopt a nestling habit or are flexible in their preferred burrowing depth [e.g., many venerids (Wells, 1957; Addicott, 1963; Frey and Basan, 1981)].* All but the smallest infaunal species will eventually be excluded once shells become so densely packed as to eliminate the soft-bottom infaunal habitat. Some inferred examples of this sequence of events are presented in the Section 4 on Miocene shell accumulations.

The exclusion of infauna by a thin but impervious shell pavement has been invoked periodically in discussions of the ecology of ancient

* Some of these species may be better treated in terms of the “tolerance model” of Connell and Slayter (1977), in which species least affected by environmental changes come to dominate the community.
shell beds, but we have not found any clear-cut examples in the literature. In fact, Johnson and Foster (1951) found a densely packed intertidal oyster bank in Hokkaido where the infaunal bivalves Tapes and Mya were living abundantly within the sediments underlying the oyster bed. Unfortunately, information on the history of the oyster accumulation and the temporal persistence of this interesting faunal association is not available. A similar situation deserving further study is the persistence of infaunal bivalves such as Chione and Mercenaria beneath Crassostrea pavements on the Gulf and Atlantic coasts (e.g., Wells, 1961; Dame, 1979; Bahr and Lanier, 1981; C. H. Peterson, personal communication, 1982). Shell pavements may cause reducing conditions in the sediments underlying them by interfering with pore-water exchange between the sediments and the overlying water column. This may have little significance for the siphonate bivalves in the preceding examples, but other taxa may be affected (e.g., meiofauna in the oyster shell experiments of Dauer et al., 1982).

Keary and Keegan (1975) speculated that shell concentrations forming at depth within the substratum were responsible for the exclusion of an infaunal Abra–Venus community on the west coast of Ireland. Although this might be an interesting example of taphonomic inhibition, the evidence presented it is at least as likely that the replacement of the bivalve community by a polychaete community was simply the result of a shift to fine sand and silt sedimentation. It seems improbable that active shallow-burrowing organisms could be driven into local extinction by a shell layer present 20 to 40 cm below the surface.

3. Expected Patterns in the Stratigraphic Record

Taphonomic feedback will be an important ecologic factor only in those benthic settings where discarded hardparts have a biologically significant duration at or near the sediment-water interface. For example, to support an epizoan community an individual shell must escape postmortem destruction long enough to serve as a site for larval settlement, growth, and repeated colonization events. At the same time, the shell must remain at the sediment surface if its colonists are to survive. In contrast to "shell islands," the persistence of individual shells is less important to taphonomic feedback within shell gravels as long as the abundance of hardparts, and thus requisite mass properties, are maintained by shell supply. However, shell gravel conditions must persist at the sediment-water interface for a period of time that is long relative to species' generation times for feedback to be manifest; even extensive shell deposits cannot influence living organisms if they are removed by deep burial from the benthic habitat.

In order to influence living biota beyond epizoan facilitation, dead shells must accumulate in abundance either on or shallowly buried within the sea floor. A great variety of biologic and sedimentologic processes are known or have been inferred to produce shell-rich deposits, either through some increase in the net rate at which hardparts are supplied to the substrate, some relative diminution in the rate of nonbiogenic sedimentation, or some combination of changes in hardpart and sediment accumulation rates (Table II). Because sedimentation ultimately determines burial rate of shell concentrations in addition to being an important factor in their formation, we use it to predict the stratigraphic distribution of shell concentrations and thus where taphonomic feedback will most significantly affect benthic communities in the marine fossil record.

* Indeed, this would represent inhibitory taphonomic feedback in the strictest cybernetic sense, with a population driving itself into extinction through the accumulation of its own hardparts.
Other processes will of course modify the stratigraphic pattern predicted from sedimentation effects alone. For example, high biological production or allochthonous supply of hardparts, independent of sediment accumulation, promote hardpart concentration (Hoskins, 1967; Rosenkrantz, 1971; Aigner, 1980a; Frey and Pinet, 1978; Kauffman, 1981); physical, biological, and chemical agents reduce shell persistence in low energy settings of delayed burial (Alexandersson, 1972, 1979; Lewy, 1975, 1981; Farrow and Cokie, 1979; S coffin et al., 1980), in high-energy settings of vigorous abrasion (Frey and Pinet, 1978; Schäfer, 1972; Chave, 1964), and in some fine-grained sediments (Aller, 1982 for marine estuarine muds; Frey and Basan, 1981 and Basan and Frey, 1977 for salt marsh muds); and organisms and short-term fluctuations in water energies exhume (or bury) hardparts despite prevailing net sedimentation conditions. Moreover, even under ideal conditions of shell concentration and persistence in a benthic habitat, the local species pool will determine how the available dead shells are utilized, if at all, by living organisms. Nonetheless, for the purposes of modeling, sediment dynamics alone provide constraints on where shell gravels and taphonomic feedback are most likely to develop in marine depositional basins.

The basin fill models of Barrell (1917), Wheeler (1964), Vail and Todd (1981), and Pitman (1978) provide a useful framework for this analysis. Given some net input of hardparts, shell (or bone) gravels will accumulate in shelf depths in the following settings, which should be considered as end-member conditions (Fig. 2).

1. Shallow-water, physically-disturbed habitats (shoreface, offshore shoals, shelf-edge shoals) in slowly aggrading depositional systems; in the stratigraphic record, these shell gravels translate into paleogeographically restricted facies within simple onlap and offlap stratigraphic sequences.
2. Benthic habitats experiencing sediment starvation, regardless of water depth; the resulting shell gravels are the stratigraphic record of marine hiatus (terminology of Vail and Todd, 1981).
3. Benthic habitats through which an appreciable sediment supply is bypassed, regardless of water depth; these shell gravels record omission due to a failure of permanent sediment accumulation.
4. Areas experiencing submarine erosion; shell gravels record erosional truncation.

In the stratigraphic record, gradations between these four end-member settings are possible because of intermediate conditions of sediment accumulation, both in time and space. Moreover, an individual shell gravel can vary in character along its lateral extent or within its thickness. Many
of the examples discussed below in fact reflect the intergradation and compounding of end-member types.

3.1. Sediment Aggradation

On graded shelves (in which sediments are in hydraulic equilibrium and become progressively finer with distance from shore), shell material will be most abundant in substrata of shallow-water environments. There, autochthonous shell production is generally high due to large biomass production (Eisma, 1966; Dorjes, 1972, 1977; Frey and Pinet, 1978; Warwick, 1980; Wigley and Theroux, 1981), high population turnover rates for some species (e.g., Vermeij, 1978; Levinton, 1970), and a wide spectrum of body sizes including large and robust specimens (Jackson, 1972, 1973). Introduction of allochthonous shell is also greatest here (Aigner and Reineck, 1982). In addition, the greater frequency, magnitude, and duration of physical reworking events that remove fine sediment produce and maintain shell concentrations near the sediment-water interface where they can be amalgamated into shell gravels (cf. Aigner, 1979, 1980b, 1982a) (Fig. 3). Although mechanical abrasion can significantly reduce net shell input to the substratum (Chave, 1964; Driscoll and Weltin, 1973), chemical conditions favorable to shell preservation are created in coarse substrata by free exchange with overlying seawater and in physically disturbed muds by high alkalinity levels (Aller, 1982).

![Facies-Model Diagram]

Figure 3. Onshore–offshore gradient in physical reworking of the sedloor and resultant shell concentrations. From Aigner (1980b) and reprinted by permission.

In contrast, deep-water mud-bottom shelf communities are characterized by low biomass production (Buchanan et al., 1978; Warwick, 1980; Flint and Rabalais, 1981; Walsh, 1981), low population turnover rates, and small body sizes compared to shallow-water sand communities. High shell production does occur locally in response to shelf-edge upwelling (e.g., Carey, 1972; Nichols and Rowe, 1977), and deep-water skeletal build-ups do provide some allochthonous supply (Wilson, 1979; Mullins et al., 1981). Allochthonous supply from nearshore sources is rare, however (Cadée, 1968; Jervey, 1974; Kreisa, 1981), and, although shell abrasion is probably low, dissolution rates are high (Aller, 1982) and bioroders and duraphagous predators active. Graded-shelf shelly bottoms represent localized biogenic concentrations or rare storm events and, once buried, should tend not to be exhumed and reworked into shell gravels (Fig. 2). Because more than 70% of modern shelf area is starved and not at grade (Emery, 1968), most modern deep shelf communities and substrata are inappropriate analogs for this usually shell-poor environment (Swift and Heron, 1969).

In the stratigraphic record, environmental differences in sediment shelliness are translated into facies differences. The result is a mosaic of shell-rich and shell-poor sedimentary volumes in which major shell gravels characterize the shallow-water margins of basins (Futterer and Paul, 1976) where they describe transgressive–regressive cycles. Simple transgressive–regressive facies patterns are most completely preserved in aggrading depositional basins where successively younger deposits either onlap or offlap older deposits (Fig. 2).

Many large-scale stratigraphic alternations of shell-rich and shell-poor strata in the fossil record have been inferred to be the product of such lateral facies migrations. For example, Schwarz (1975) recognized a transgressive–regressive sequence in the Triassic Muschelkalk of Germany in which a nearshore shell bank environment was responsible for shell-rich intervals. Similarly, the Neogene of the North Sea Basin contains a nearshore shelly sand facies (the “Coralline Crag” facies) that stratigraphically alternates with and laterally interfingers with a much less fossiliferous offshore clay and an unfossiliferous continental facies (Zagwijn and Doppert, 1978; Van Staadenin et al., 1979) (Fig. 4).

3.2. Sediment Starvation

During a rapid rise in sealevel, terrigenous sediment supply to a basin is much reduced or eliminated through river and coastal trapping of sediment (Swift, 1976; Ryer, 1977; Pitman, 1978). Sediment supply can also be cut off through simple rerouting and, on a longer time scale, from
Figure 4. Shell accumulation in nearshore, shallow-water environments in an aggradational regime, as exemplified by the Neogene Coraline Crag, northwestern Europe. From Zagwijn and Doppert (1978) and reprinted by permission.

... diminishing relief in source areas. Under such conditions of sediment starvation, hardparts passively accumulate in deep-water as well as shallow-water environments due to deprivation of diluting sediment (Fig. 2). Starved shell gravels thus have potential for great lateral extent within the basin, unlike the facies records of shallow-water environments which are paleogeographically restricted at any given time. Because of their bathymetric range of formation, lateral variation in species composition should be expected in starved gravels; vertical variation will also result if water depths in the basin change during the starved regime. These gravels are the record of marine hiatuses (Vail and Todd, 1981); in any single event, starved conditions are initiated first in offshore (most distal) areas where they also persist longest.

As previously mentioned, more than 70% of modern continental shelf areas are presently experiencing a regime of sediment starvation (Emery, 1968), and these shelly sediments provide ample opportunity for taphonomic feedback. Most of the modern offshore shell gravel communities described in Section 2.1 owe their existence to starved conditions.

Reif (1971) describes a bone bed between the Triassic Muschelkalk and Keuper of Germany that he infers to have formed through sediment starvation. The bed is composed of hardparts produced during the starved period and pre-fossilized bone material exhumed from the seafloor during an initial erosional phase [but see Reif (1982) for explanation in terms of episodic storm reworking]. Sediment starvation was also the probable mode of formation of a rich, extensive bone bed in the Miocene Calvert Formation of Maryland (Myrick, 1979). The 0.5-m-thick, glauconitic bone bed contains a condensed record of marine mammals from several ecologically distinct and temporally successive populations.

The starved basin concept was introduced originally for deep unfilled basins surrounded by sediment-hoarding epicontinental shelves (Adams et al., 1951). Adams et al. believed that the starved conditions of the central Midland Basin of Texas, which has a Pennsylvanian record only one-tenth as thick as coeval shelf deposits, were produced by a combination of rapid subsidence that outstripped the rate of carbonate production, and great distance from shoreline sources of terrigenous sediment. In this and classic starved sequences from pelagic settings (Heim, 1924, 1958; Jenkyns, 1971), fossil material is generally rare except for local occurrences of nektic and planktic hardparts because of inhospitable benthic conditions (specifically soft substrata and low oxygen levels). Taphonomic feedback is thus expected to be minimal in these very-deep-water, off-shelf settings, except perhaps for instances of epizoan facilitation by individual shell islands. Feedback should be most significant and complex in shallower water-starved settings where shell gravels will be most fully developed.

3.3. Sediment Bypassing

Resumption of an appreciable sediment supply to a starved shelf initiates basinward progradation of a sedimentary wedge (e.g. delta or continental shelf; Fig. 2). When a toposet horizon of such a wedge is maintained at the seafloor surface, net sedimentation there will be relatively low because of hydraulic bypassing of sediment to the leading depositional edge. Maintained for a sufficient period of time, a winnowed shell-rich deposit will form and grow laterally out into the basin as the wedge progrades.

As the sedimentary wedge advances basinward, it encroaches upon sediment-starved distal deposits. The preceding regime of shell concentration by sediment starvation is thus progressively replaced by a con-
diation of sediment aggradation, and eventually by shell concentration through sediment bypassing (in progress in part 3 of Fig. 2). As an example, the Mississippi River delta is presently building outward over a relict shelf shelf pavement created by starvation during the Holocene rise in sea level (Coleman and Gagliano, 1965; see also Morton and Winkler, 1979). We are unaware, however, of any evidence for a shell or bone concentration in delta-topsets. This lack may be a consequence of the tremendous sediment supply to the delta and its isostatic subsidence in response to that sediment load; residence time of any single horizon or locus of fossil concentration near the sediment—water interface is apparently too low given the supply of hardparts.

In contrast, from the Triassic of Germany, Aepler (1974) describes a bone bed condensed through the lateral amalgamation and basinward extension of lenses of rivermouth gravel that contain bones derived from fluvial and lagoonal sediments (Fig. 5). Unlike the modern Mississippi delta, hardpart supply was sufficient to produce fossiliferous lenses, and a lower rate of sediment input and isostatic subsidence permitted the amalgamation of these lenses into a nearly continuous horizon of hardparts along the topset beds of the condensed deltaic record. Shell and bone deposits produced under bypass conditions should provide opportunities for taphonomic feedback but may be difficult to detect in the fossil record due to prolonged reworking of early and late generation hardparts during the progressive winnowing process.

Continental shelves of course are themselves sedimentary wedges extending into deep, starved ocean basins, and, when at grade, they also prograde by the partial or complete bypassing of shore-derived sediment supply. Exceptionally, a shelf-wide shell gravel can arise through bypassing when a single horizon persists at the seafloor because eustatic fall precisely matches subsidence. A relative acceleration in eustatic lowering would bring about the erosional removal of the concentration; a slowdown in sealevel fall would arrest hardpart concentration by burial. All three situations—progradation accompanied by bypassing, erosion, or aggradation of the shelf surface—have been recognized in seismic sections (e.g., see illustrations in Vail et al., 1977). Like the smaller-scale deltaic situation, a critical balance between subsidence and eustatic sealevel fall is essential for the concentration of hardparts by sedimentary bypassing.

Midslope settings are another site of shell concentration by winnowing and sedimentary bypass. Baird (1961) and Baird and Brett (1981) document steinkern concentrations colonized by epifauna in the Middle Devonian Hamilton Group of New York. They attribute these diastogenic concentrations to erosional reworking and accumulation under a downslope erosion model whereby sediments suspended by bioturbators are removed by weak slope currents.

![Figure 5. Formation of the Rheetic Bone Bed (Triassic, Germany) through sediment bypassing during the accumulation of a condensed deltaic record. River-mouth gravel concentrations amalgamated laterally as the delta prograded; the seaward edge of the bone bed was later reworked during an erosional transgression. From Aepler (1974) and reprinted by permission.](image)

### 3.4. Erosional Truncation

Erosional reworking can precede or terminate regimes of starvation and bypassing, and can precede or follow upon the lateral migration of a high-energy, shell-rich facies. Shells concentrated during erosional events are derived from: (1) exhumation of previously buried material; (2) in situ biological production contemporaneous with erosion; and (3) delivery of allochthonous hardparts from adjacent areas.

High-energy conditions necessary for erosion are usually limited to a relatively narrow belt along basin margins and to localized, paleotopographic highs on the deeper seafloor. The resulting shell gravels are thus facies records of erosion that is paleogeographically restricted at any given time. In a situation of erosional transgression, for example, a shell-rich lag accumulates on the ravinement surface, deposited in the wake of a landward-advancing suite of high-energy environments (e.g., Ryer, 1977). Eroded sediment is transported seaward and accumulates on the trailing edge of the transgressive shell deposit.

The formation of Holocene shelf gravels involved such an initial erosional stage, although their continued formation to the present day has
resulted from sediment starvation (Section 3.2). Interestingly, Pilkey et al. (1981) found that reworked Tertiary shells are not preserved in the basal deposits of the Holocene shell gravel of the Georgia Shelf. Instead, all shell material reflects biological production and allochthonous shell delivery during the post-erosion period of starvation. Shell-rich Holocene shelf deposits of western Africa, New Zealand, and Scotland were also concentrated during high-energy conditions associated with erosional transgression and subsequent sediment starvation (Norrish, 1972; Eisma et al., 1976; Farrow et al., 1978; Andrews, 1979). As an ancient example, the basinward portion of the Triassic delta-top bone bed described by Aepler (1974) (Section 3.3) (Fig. 5) also underwent erosional reworking during marine transgression, resulting in a basin-floor concentration of prefossilized vertebrate material previously concentrated by delta-top bypassing.

Erosional truncation of strata can, of course, accompany regressive depositional sequences as well as transgressive sequences. For example, a drop in relative sea level during delta progradation would cause destructive reworking of delta-top shell gravels because of erosional truncation of the delta itself (Fig. 2). This cannibalization would proceed in a basinward direction, opposite to that of erosional transgression; reworked hardparts and sediment are transported seaward where they accumulate in a prograding deposit which is itself reworked eventually. In all situations, erosional exhumation and concentration of hardparts and pre fossilized material from earlier deposits, affording opportunities for taphonomic feedback, is restricted at any given time to a relatively narrow band of high-energy environments.

3.5. Discussion

Because of the scale of the mechanisms involved (eustasy, basin subsidence, total basin sediment supply), examples of the four kinds of shell gravels described above can be assumed to have sufficient duration as benthic habitats to influence living organisms. The areally most extensive shell gravels should result from sediment starvation and, under special circumstances, sediment bypassing affording opportunities for taphonomic feedback over a broad range of bathymetries, water energies, light intensities, and primary productivities. For example, Schäfer (1973) describes lateral variation in the paleoecology and taphonomy of a shell bed that extends continuously across three hydrographic zones within the Upper Muschelkalk basin of Germany (Triassic). In contrast, shell gravels generated on aggrading shelves during onlap or offlap are restricted bathymetrically to localized areas and the particular species pools that characterize those physical settings. Shell gravels having most limited lateral extent at any given time are those produced by submarine erosion, which proceeds only in the most high-energy settings.

Spatial and temporal variation in the dynamics of sedimentation has potential to create shell gravels of compound nature. For example, the Holocene shell gravel record of modern continental shelves accumulated in response to early transgressional erosion followed by sediment starvation; and the landward portion of the Triassic bone bed described by Aepler (1974) originated through sedimentary bypassing whereas its basinward portion experienced an additional phase of reworking because of later erosional truncation. Evidence of taphonomic feedback will vary both vertically and laterally within such compound shell gravels as a consequence of their mixed origins.

On a day-to-day, organismal time scale, the dynamics of hardpart accumulation probably differ more by degree than type among the shell gravel settings. By dynamics we mean: Did shells accumulate in isolated patches or as a widespread carpet, on the seafloor surface or at some shallow depth within the sediment? Were they continuously exposed or periodically buried? Did shell packing density in the sediment develop instantaneously through some catastrophic event, or gradually over a period of several generations or more? Sediment starved conditions should differ most from the other settings, both taphonomically and ecologically. At shelf depths, however, an allochthonous sediment supply does not disallow hydraulic reworking of previously deposited sediment [e.g., palimpsest sediments of modern Atlantic shelf (Swift et al., 1972)]. Repeated exhumation—burial cycles, for example, may thus be no less frequent on starved shelves than on bypassed shelves of similar depth and oceanographic facing. Pelagic settings of sediment starvation should on average experience less-frequent reworking events. Further research is needed to determine how and to what degree shell gravel settings are distinguished in terms of short-term sediment dynamics and taphonomic feedback. Some preliminary observations on Miocene shell deposits are presented in Section 4 (see Fig. 9).

The genetic bone bed classification of Aepler and Reif (1971) describes hardpart accumulations that fall into the starved, bypass, and erosion categories identified above. These are Kondensationbonebeds (equivalent to starved condition), Seifenbonebeds (subset of bypassed condition), and Transgressionsbonebeds (subset of erosional condition). Prolonged, reduced sedimentation of any type will eventually yield a hardpart concentration consisting primarily of bone material due to its great durability. Like shells, bones can serve as sites of endo- and epibiont infestations when burial is delayed (e.g., Frey et al., 1975; Antia, 1979). We are unaware, however, of situations where bone abundance in the
substratum was sufficient in itself to inhibit soft-bottom and/or facilitate coarse-bottom species.

Shell gravel development is temporally and spatially patchy in relatively shell-poor sediments, so that taphonomic feedback there will commonly be restricted to epizoan colonization of single shell substrata. Such shell-poor sediments accumulate in (1) lower-energy environments within slowly aggrading depositional systems, where physical reworking of sediments is infrequent and shell input low; (2) environments of all but perhaps highest energy within rapidly aggrading systems; and (3) dysaerobic and anaerobic environments not receiving significant allochthonous hardparts (compared to rate of net sedimentation) from adjacent benthic environments or from nektos/plankton. These settings encompass the vital- and lethal-pantostrate biofacies of Schäfer (1972). This restriction in taphonomic feedback is in contrast to the extensive and community-wide operation of both facilitative and inhibitory feedback expected in settings of prolonged, pervasive shell gravel development such as enumerated in the preceding sections. Those shell gravel habitats will have the characteristics of Schäfer's (1972) vital- and lethal-pantostrate biofacies.

4. Case Study: Neogene Chesapeake Group, Atlantic Coast Plain

The Middle Miocene Calvert and Choptank formations of the Chesapeake Group, Maryland and Virginia, comprise 70 m of terrigenous fine sands and silts reworked for their diverse and well-preserved macroinvertebrate faunas (Clark et al., 1904; Gernant, 1970, 1971). These include: abundant aragonitic and calcitic molluscs and less common echioids, barnacles, bryozoans, and corals; phosphatic inarticulate brachiopods and decapods; and a variety of biogenic traces. Bones and teeth, particularly from marine mammals, are also sparsely represented throughout and common at certain horizons (Whitmore, 1971, and references therein). Because hardparts occur not only as disseminated material but in densely packed shell beds at a variety of scales, a diversity of taphonomic feedback types and intensities can be expected. The following observations are the result of a detailed analysis of the shell beds and their stratigraphic context, based on 194 measured sections distributed throughout the 9000-km² outcrop area (Kidwell, 1982b) (Fig. 6).

Shell accumulations in the Calvert and Choptank formations are readily classified into two descriptive categories—minor simple and major complex shell beds—according to differences in physical scale and internal complexity (Kidwell, 1979, 1982a,b). Minor simple shell beds are relatively thin accumulations that are restricted in lateral extent to individual lithofacies and exhibit little or no variation in paleontologic faunal composition, sedimentary matrix, or internal structure either vertically or laterally. By analogy with modern examples, all are inferred to record single, geologically brief episodes of shell concentration achieved through some biologic, sedimentologic, or combination of biologic and sedimentologic processes. These processes include: gregarious behavior; mass mortality; predator or scavenger activity; diastemetic sedimentary omission; storm winnowing; localized scour; introduction of allochthon-
ous shell; and hydraulic reworking of an originally biogenic concentration.

In contrast, major complex shell beds are thick, tabular deposits (1 m to 10 m locally) whose great lateral extents (to 9000 km²) exceed those of contiguous, less-fossiliferous facies. Each complex shell bed rests on an erosional disconformity, incorporates many amalgamated or condensed minor simple shell beds in microstratigraphic sequence, and exhibits lateral variation in overall thickness, lithology, internal structure, and in the composition and thickness of microstratigraphic parts. Vertical telescoping of hardpart concentrations, documented by lateral tracing of the major shell beds into thicker sections, and the winnowed sand matrix of the shell beds indicate a primarily sedimentologic origin. Each of the major shell beds records erosion followed by a period of reduced net sedimentation resulting in the condensation of hardparts from a transgressive sequence of marine environments. The major complex shell beds are thus most analogous to shell deposits produced by the most recent, Holocene transgression.

The laterally extensive major shell beds (and a thin bone bed) alternate stratigraphically with less-fossiliferous muddy intervals containing discrete, minor simple shell beds. The basal disconformities of the major shell beds subdivide the section into a series of depositional sequences.
each of which exhibits (1) overall fining up in the terrigenous matrix, (2) reduction in hardpart abundance, and (3) with one exception, a cyclic sequence of deepening-up then shallowing-up environments (Fig. 6).* Shallowing phases, attaining depths as shallow as those at which the preceding deepening phase began, are, in all examples, represented by shell-poor muddy sediments rather than by a shell-rich winnowed deposit such as characterizes deepening phases. This asymmetry in deposition and thus in substratum type is illustrated schematically in Fig. 7, and represents a modification of the starved setting described in Section 3.2.

4.1. Evidence of Taphonomic Feedback

Most examples of minor simple shell beds lack evidence of interactions between living biota and dead shells. For example, in very muddy facies of the PP-2, PP-3, and CT-1 depositional sequences (Fig. 6), the infaunal bivalve Glossus fraterna occurs as disarticulated, uninfested, and primarily convex-up specimens in monospecific shell stringers (pavements). Although the periostracum would have protected the exterior shell surfaces of Glossus from epibenthic attack, the pristine interior surfaces and sedimentologic features of the shell bed argue against prolonged accumulation of shells on the seafloor: the sedimentary matrix of each stringer is identical with the surrounding strata, and neither firmgrounds nor discrete erosional surfaces are associated with the stringers. Unlike classic storm-produced shell beds capped by physically laminated sediment (cf. Aigner, 1979), the Glossus stringers float within a uniformly and totally bioturbated sedimentary matrix.

As additional examples of minor simple shell accumulations, the infaunal gastropod Turritella plebeia occurs in paucispecific stringers with most specimens preserved in life position (PP-3 sequence of the Calvert Formation). Associated with Turritella are sparsely disseminated and disarticulated G. fraterna, fragments of a bilaminar foliate bryozoan, small specimens of the scallop Chesapeken nefrens, and, between stringers, articulated specimens of the lucinid bivalve Lucinoma contractus in life position. The lack of bryozoan attachments and the presence of mobile epifauna and infauna indicates that the Turritella shells served neither as substrata for nor as inhibitors of co-occurring organisms. The presence of shells in life position and their occurrence within beds rather than on bedding surfaces corroborates that the shells were buried rapidly with little or no reworking.

* Because marginal marine as well as open marine environments are represented, not every deepening-then-shallowing cycle represents a transgressive–regressive cycle (see Kidwell, 1983).
Faunal composition does change vertically within one minor shell bed in the Calvert Formation (PP-2 sequence). The upper 25 cm of this Chione-dominated accumulation contains a distinct, more diverse molluscan assemblage occurring in small (less than 10 cm) clean sand pods. However, upon close inspection, these pods can be recognized as burrows filled with shelly sand from the overlying unit. The vertical trend of increasing species richness through the Chione shell bed is thus not a biotic response to the progressive concentration of shells in the substratum (i.e., taphonomic feedback), but is the result of injection of a later, ecologically unrelated assemblage. This process of vertical admixture is comparable in scale to the process of faunal condensation discussed by Fürsich (1978).

An unusual example of taphonomic feedback within a minor simple shell bed occurs in the PP-1 depositional sequence of the Calvert Formation, where a stringer of T. plebeia served as a substratum for sheets of encrusting bryozoans (Kidwell, 1982b). Unlike typical Turritella stringers, which lack evidence of feedback, these specimens have been rotated from life position into a concordant alignment and are associated with a firmground, recognized by its Glossifungites trace assemblage (cf. Frey and Seilacher, 1980). Associated molluscan species are discreticulate and reoriented within the stringer, further suggesting postmortem reworking of the shells that would have prolonged their exposure on the seafloor and thus permitted epizoan colonization. This is an exceptional occurrence, however, and other minor simple shell beds associated with bedding plane surfaces (tabulated in Kidwell, 1982a,b) lack evidence of taphonomic feedback.

Evidence for taphonomic feedback in major complex shell beds consists of (1) endo- and epibiotic infestation of infauna, and (2) a qualitative correlation between shell-packing density and the relative abundance of soft-bottom and shelly-bottom species. Shell-packing density is < 5–20% shell by volume in shell-poor interbeds within the major shell beds, but attains values of 40–60% in the shelliest parts of the beds.

Borers and encrusters occur on both epifaunal and infaunal species and include: bore scleractinian colonies; attachment scars, basal plates, and articulated specimens of balanid barnacles; encrusting hydroidinian colonies; and borings resembling those of the modern spionid polychaete Polydora, clionid sponges (at least two species), pholad bivalves (Martesia and Zirfaea), and undifferentiated fungi and algae. Because of uncertainty in distinguishing pre- and postmortem infestations in many epifaunal specimens, the frequency of infaunal infestation is probably a better index of shelly seafloor conditions.

Epi- and endobionts are infrequent on infaunal specimens in relatively shell-sparse deposits, never exceeding 5% of individuals in three surveys totaling 380 specimens (Kidwell, unpublished data). Infestation is more frequent in densely fossiliferous units, ranging from 10% in one 90-specimen sample, to more than 60% of recognizable specimens in selected horizons within the most densely fossiliferous parts of the Drumcliff and Camp Roosevelt shell beds. Clionid sponge and spionid polychaete borings are the most common evidence of epizoans in all of the major shell beds. Because of the disintegration of bored shells into unrecognizable shell fragments, measured frequencies in the most shell-rich beds are probably minimum estimates of true infestation.

A correlation between shell-packing density and faunal composition is apparent both microstratigraphically and laterally within the Drumcliff shell bed (CT-0 sequence; Fig. 6). In the southern Calvert Cliffs, the uppermost 2 m of the shell bed consists of a clean fine sand containing less than 15% shell, which occurs in distinct shell layers and as sparsely disseminated whole and broken specimens (Fig. 8). The fauna is dominated numerically by soft-bottom gastropods Turritella and Lunatia and bivalves Glossus, Bicorbula, Anadara, Cerastoderma, Lucinoma, Phacooids, and Panopea. Turritella and Glossus alone compose more than 85% of the fauna in several exposures. Less common are taxa whose modern representatives are known from a range of substrata, e.g., the infaunal bivalves Mercenaria, Eucrassatella, Astarte, Dosinia, and Cystoides, and small specimens of the scallop Chesepeack.

The lower part of the Drumcliff shell bed, a very densely packed clean fine sand containing abundant broken and whole shells (Fig. 8), contains all of the soft-bottom taxa found in the upper part of the shell bed, along with a number of other typically soft-bottom forms including Gari, Asaphis, Nucula, Yoldia, Diplodonta, Macoma, Semel, Atrina, Caryocorbula, and Spisula. However, Mercenaria, Eucrassatella, Astarte, Dosinia, Macrocallista, and Chesepeack are much more abundant, and unlike the less densely packed upper part of the shell bed, the fauna also includes species characteristic of firm, shelly, and hard substrata. These include: epifaunal gastropods Diadroma, Crucibulum, Echphora, and Busycna; attached Vermetus (gastropod), Anomia (bivalve), Astralina (coral), Balanus, and byrozoans; endobiotic Martesia and Zirfaea (pholad bivalves) and clionid traces; and nesting or semi-infaunal bivalves Hiarella, Carditamera, Petricola, Mytilus, and Isognomon.

A similar biofabric–fauna correlation is evident in exposures of the Drumcliff shell bed westward along strike from the Calvert Cliffs in the Patuxent River area. There, the Drumcliff shell bed can be subdivided into three facies (Kidwell, 1982b): (1) a relatively sparsely fossiliferous clean sand with a largely infaunal assemblage dominated by soft-bottom taxa (Turritella, Macoma, Phacooids, Bicorbula, etc.), with the very shell-rich layers within this sand containing abundant Chesepeack or Isognomon with Balanus, Astralina, Martesia, and clionid traces; (2) a densely fos-
Figure 8. Representative stratigraphic sections of the Drumcliff, Camp Roosevelt, and Boston Cliffs major complex shell beds, and of the Camp Roosevelt-Barren interval transition. After Kidwell (1982b). Vertical scale in 0.5 m intervals. Lithology of sedimentary matrix indicated by c (= clay), s (= sand), and ss (= silty sand), and by lab analysis (sand mode in phi units [ø]: percentage admixed fines < 62 μm). Only dominant fauna are noted. An, Anadura; Ano, Anomia; Ast, Astorite; Asth, Astridella; Att, Atrio; Bal, Balanus; Bic, Bicorbula; bry, bryozoans; Card, Carditumera; Cer, Cerastoderma; Ch, Chione; Chp, Chespucete; Cli, Cliona borings; Cruc, Crucibulum; Cyclo, Cyclocardia; Dent, Dentillium; Die, Diodyra; Dos, Dosinia; Ecp, Echore; Eu, Eucriassatella; Gl, Glossus; Gly, Glycymes; hydr, hydroclitid; isog, Isogonon; Kuph, Kuphus; Luc, Lucinoma; Macr, Macrocallista; Merc, Mercenaria; Mod, Modiolus; Myt, Mytilus; Ost, Ostrea; Pan, Panopea; Petr, Petricola; Phac, Phacoides; Tur, Turritella; Ver, Vermetus. Sections measured in Calvert Cliffs except for Boston Cliffs shell bed measured at type section on Maryland Eastern Shore.
siliferous clean sand dominated by large Isognomon, Chesapeake, and Placophen with Astrhelia, Balanus, Martesia, and clionid borings; (3) a densely packed clean fine sand with a mixed epifaunal-infaunal assemblage of molluscs and spathangid echinoids that is nearly identical to the shell gravel assemblage present in the lower part of the Drumcliff shell bed in the Calvert Cliffs. This grades into a less fossiliferous interval of sand dominated by Anadara, Bicorbula, Lucinoma, and Asparta.

In contrast to the Drumcliff shell bed, the Camp Roosevelt shell bed (PP-1 sequence, Calvert Formation) is densely fossiliferous and fragmental throughout its 3-m thickness (Fig. 8). Its fauna is very similar at the generic level to that of the lower part of the Drumcliff shell bed in the Calvert Cliffs, but in addition includes abundant Glycymeris, a nesting species of Anadara, more abundant bryozoa, and diverse muricid gastropods. Encrusting hydactinians and tube-constructing terebrinid bivalves ("Kuphus") are also present. Large-bodied infauna typical of shell-free substrates are less common and restricted mostly to the lower 1 m of the Camp Roosevelt shell bed. These include Cerastoderma, Dosinia, Atrina, Phacoideas, and larger specimens of Glossus. A second species of Turritella, two small species of Chione, and another corbulid bivalve contribute to the diversity of small-bodied, soft-bottom taxa.

The densely fossiliferous Camp Roosevelt shell bed grades into an overlying barren clay through a transitional interval of interbedded clean sand and silty sand (Kidwell, 1982b) (Fig. 8). The 10- to 20-cm-thick sand beds are moderately fossiliferous and are characterized by all or some of the following taxa: Chione, Asparta, Turritella, Mercenaria, Anadara, Cerastoderma, Atrina, Panopea, Spisula, Caryocorbula, and Dentalium (scaphopod). Bryozoa and juvenile or very small adult specimens of Anomia, Ostrea, Chesapeake, and Crucibulum co-occur in some of these sandy shell layers. Intervening silty sands contain sparse, finely fragmental shell and small disarticulated specimens of Turritella, Asparta, Chione, Anadara, Anomia, Chesapeake, and others; Nucula and tellinid bivalves are also present, some in living position.

Semi-infaunal, epifaunal, and epizoan species are relatively more abundant in the Boston Cliffs shell bed than in the other major complex shell beds, and in many layers attain a clear dominance both in terms of diversity and abundance. Taxa include: Chesapeake, Isognomon, semi-infaunal Anadara, Anomia, Ostrea, Carditamera, Crucibulum, Echahora, Mytilus, Balanus, Astrhelia, bryozoa, and spionid and clionid borings. With the exception of Mercenaria and Dosinia, both adaptable to shelly substrata (e.g., Stanley, 1970), and Cerastoderma and Eucrassatella in less fossiliferous beds, infaunal species tend to be small-bodied (Asparta, Pitar, Caryocorbula, Turritella, Nucula, Semele, Gari, Bicorbula, Polinices, Lunitia, Macoma, Asaphis) (data from type section; Kidwell, 1982b) (Fig. 8).

The upper 1 to 2 m of this spectacular shell bed is composed almost entirely of disarticulated and articulated specimens of the robust scallop Chesapeake, many of which exceed 15 cm in diameter. These scallops support dense and multiply-recruited barnacle colonies which in turn encrust with bryozoa and penetrated by clionid borings; oyster attachment scars are also common on the scallops.

4.2. Discussion

The higher incidence of epi- and endobionts and of shelly-bottom species in the most densely packed shell layers of the major complex shell beds indicates that those layers record shell gravel benthic habitats rather than 1) concentrations that were created catastrophically and buried immediately, or 2) concentrations that accumulated slowly but in the absence of living organisms. The dynamics of shell gravel accumulation did vary among the major shell beds, however. Larger-bodied soft-bottom infauna are more abundant and pervasive through densely fossiliferous parts of the Drumcliff shell bed than in the Camp Roosevelt and Boston Cliffs shell beds, for example. This suggests either that shell gravel conditions were never fully realized during Drumcliff accumulation, or that intermittent soft-bottom conditions permitted the repeated colonization and development of soft-bottom communities. Numerous burrowed, scarred, and corroded discontinuity surfaces within the Drumcliff shell bed argue in favor of alternating soft and shelly seafloors during shell bed accumulation (Fig. 9). Such a pattern of shell bed accumulation would explain the lack of an overall trend of infaunal inhibition through the densely fossiliferous facies of the shell bed. This pattern of alternating soft and shelly bottoms is similar to that found by Aigner (1982b) in complex moluscan shell accumulations from the Eocene of Egypt.

Shelly- and hard-bottom taxa are diverse throughout the Camp Roosevelt shell bed, while the soft-bottom infauna are almost invariably restricted to small-sized species and to small specimens of larger-sized species; fossil assemblages intergrade microstratigraphically through the shell bed, interrupted by only a few bedding discontinuities. These features suggest that shell gravel conditions were maintained more continuously on the Camp Roosevelt seafloor than on the Drumcliff seafloor (Fig. 9). These shell gravel characteristics are taken even further in the upper Boston Cliffs shell bed, which culminates in an epifaunal Chesapeake community.

Soft-bottom conditions no doubt existed intermittently during accumulation of both the Boston Cliffs and the Camp Roosevelt shell bed. In fact, some veneer of mobile sediment is practically required in order
to explain the fairly low levels of bioerosion through much of the sequence. Unlike those of the Drumcliff seafloor though, transient sedimentary increments were apparently too thin and/or too temporary to permit full development of soft-bottom communities (Fig. 9).

While overgrowth relationships and sequential colonization are often readily observed in situations of epizoan facilitation, taphonomic feedback within ancient infaunal communities is difficult to demonstrate since later species utilize the same sedimentary volume as earlier species.

Added to this is the obscuring effect of vertical admixing through physical and biogenic reworking. Several lines of evidence lead us to believe, however, that the co-occurrence of soft-, firm-, and shelly-bottom taxa in shell gravel sediments records the progressive alteration of benthic communities through taphonomic feedback.

1. A direct relationship exists between the scale of hardpart accumulations and the dominance of shell gravel faunas. Minor simple shell beds, including those found in very muddy stratigraphic intervals and those from less fossiliferous beds within the major complex shell beds, are composed almost exclusively of soft-bottom taxa (corbulids, Turritella, Glossus most typical) (Kidwell, 1982a,b). Thicker and laterally more extensive deposits, better described as patchy shell gravels than shell pavements, contain soft-bottom taxa plus taxa preferring but not restricted to firmer substrata (venerids and astartids, for example). Such accumulations include less fossiliferous sand facies of the Drumcliff shell bed and sandy interbeds in the Camp Roosevelt–Barren interval transition. Finally, the most densely fossiliferous and largest scale shell gravels are characterized by shelly bottom faunas accompanied by abundant soft- and firm-bottom species. Since dense shell gravels build up through time (each Miocene example can be demonstrated to be a vertically telescoped and condensed series of many minor simple shell beds; Kidwell, 1982a,b), the sequence of faunal change appears to be from soft- to firm- to shelly-bottom adaptive types during the progressive development of any single shell gravel.

2. The ecologically mixed character of the faunas cannot be attributed to post-mortem transportation. The shell gravels are in-situ deposits, rather than allochthonous or mixed autochthonous—allochthonous concentrations of hardparts. Although many of the soft-bottom taxa are out of their usual muddy lithologic context, neither soft-bottom nor shelly-bottom groups exhibit transportation effects (such as low articulation frequencies, strong size sorting). Nor do sedimentary structures indicate hydrographic conditions adequate for shell transport: actupaleontologic investigations have demonstrated that significant between-habitat transportation of shells is rarely achieved in the absence of strong directional currents (e.g., turbidity and rip currents; Jersey, 1974; Johnson, 1965; see review by Kreiss, 1981). Even in high-energy settings and under storm conditions transportation is often limited to epifaunal forms (Cadée, 1968; MacDonald, 1976).

Stratigraphic context also argues against between-habitat transportation of shells in the Miocene deposits. Faunal diversities in the less fossiliferous strata truncated by or in lateral relation to the major complex shell beds are totally inadequate in all examples to have served as allochthonous sources for the hardparts, and since the major complex shell beds or their microstratigraphic parts can be traced laterally into depo-
sitional pinchouts (Kidwell, 1982b, 1983), invoking some subsequently-destroyed source area is difficult to justify. Without a allochthonous or older source of hardparts, a catastrophic origin for the major shell gravels is less likely than a gradual, in situ process of accumulation; long-term shifts in faunal composition in response to habitat alteration are thus feasible.

3. The correlation between shell packing density and faunal composition is not simply a by-product of population growth rates. Opportunistic species [recognized by Levinton's (1970) criteria] are common as monospecific stringers in shell-poor intervals, whereas the major contributors to the densest shell beds are nonopportunist taxa exhibiting evidence of long life spans (e.g., annual growth rings, massive shells). The densely fossiliferous intervals thus cannot be explained simply in terms of an explosive influx of species having high shell production rates.

4. The greater representation of shell gravel infauna and epifauna in the densest shell accumulations suggests a directionality in faunal change that is consistent with live–dead interactions but not expected from live–live interactions. Live mobile infauna are unlikely to facilitate epifauna; in fact, they frequently have an inhibitory effect on live epifauna through disturbance during bioturbation (e.g., Rhoads, 1974; Brenchley, 1981b). By the same token, inhibition of infauna by living epifauna would require improbably high epifaunal population densities before suspended food or access to the water column (or to sediment during larval colonization) became limiting. Furthermore, epizoans on infaunal shells and on the interiors of epifaunal shells not only provide indirect evidence for live–dead interactions, but demonstrate that discarded shells remained near the seafloor surface and thus ecologically influential for some time after death.

As a mechanism of faunal change in benthic communities, taphonomic feedback can be either autogenic or allogenic. In the muddy intervals of the Calvert and Choptank formations (Fig. 6), taphonomic feedback was recognized in only one of the minor simple shell beds—a layer of reworked Turritella encrusted by bryozaons. The winnowed sand matrix and sharp lithologic contacts of this concentration indicate that a change in physical environmental conditions, specifically an episode of seafloor winnowing, was required to produce the shell concentration that facilitated epizoan colonization. In this instance, taphonomic feedback was a mechanism of allogenic faunal change. Aigner (1982b) recognized an analogous process in the colonization of storm-generated shell grounds in the Triassic of Germany and Eocene of Egypt, referring to these as "pseudo-successions".

Minor simple shell beds formed by in situ biological production alone (attritional or mass death, gregarious associations, opportunistic blooms) provide opportunities for autogenic faunal change through taphonomic feedback. These biogenic shell concentrations as well as all minor allogenic concentrations (concentrations of sedimentologic or mixed sedimentologic–biologic origin) lack evidence of taphonomic feedback, however, with the one exception described above. Possible explanations include: rapid, deep burial curtailing shell residence time on the seafloor; mobile sedimentary veneer excluding epizoans; inadequate lateral extent, thickness, or shell density to support shell gravel community; or some combination of the above.

The depositional shift from muddy intervals with their widely spaced minor simple shell beds to major complex shell beds is accompanied by an allogenic faunal change on a scale commonly referred to as faunal or community replacement (e.g., Boucot, 1979; Hoffman and Narkiewicz, 1977; Hickey and Younker, 1981). Within the major complex shell beds, physical events of seafloor reworking, winnowing, and deposition, although smaller in scale, controlled most faunal change. This effect is seen most pervasively in the Drumcliff shell bed, where alternating physical conditions are recorded in the many discontinuity surfaces that microstratigraphically subdivide and separate fossil assemblages. In contrast, the uppermost, Chesapeake-dominated section of the Boston Cliffs shell bed is microstratigraphically unbroken and probably reflects conditions created and maintained by autogenic processes, with taphonomic feedback promoted by the gregarious behavior of the large-shelled scallops within a relatively constant sedimentary regime of low total and low net rates of sedimentation.

5. Conclusions

The depositional histories of discarded hardparts have ecological consequences beyond the conventional taphonomic concerns of post-mortem information loss. Discarded hardparts have the potential to alter the composition and dynamics of benthic communities by changing the character of the physical habitat. In addition to serving as sites for epizoan colonization, dead shells facilitate and inhibit different adaptive types by altering bulk properties of the substratum, thus increasing topographic complexity and stability of the seafloor surface, increasing resistance to infaunal penetration and locomotion, and, at maximum shell abundance, restricting infaunal habitat space. We refer to both the direct and the indirect influence of discarded hardparts on living organisms as taphonomic feedback.

To a first approximation, the occurrence of taphonomic feedback in the stratigraphic record can be modeled in terms of sediment dynamics, since most forms of feedback require that hardparts both accumulate in abundance and reside on or near the seafloor surface. Taphonomic feedback will thus most strongly influence benthic community composition.
in settings of prolonged shell gravel accumulation. These include: (1) shallow-water environments where biological production of hardparts is high and the seafloor is reworked frequently; (2) environments experiencing a regime of sediment starvation in which terrigenous sediment is not supplied and so cannot dilute shell input; (3) environments experiencing a regime of sediment bypassing, in which sediment, although supplied, fails to accumulate permanently; and (4) environments experiencing a regime of submarine erosion, in which previously buried hardparts are exhumed and concentrated along with contemporaneous autochthonous and allochthonous material. In relatively shell-poor sediments, such as found in slowly aggrading quiet-water environments and in areas experiencing a great net rate of sediment aggradation, shell gravel development is temporally and spatially patchy, so that taphonomic feedback will commonly be restricted to epizoon colonization. This pattern in the occurrence of taphonomic feedback—in frequent and limited in shell-poor strata, and extensive and community-wide in densely fossiliferous strata—is clearly evident in the Miocene Chesapeake Group.

Taphonomic feedback deserves explicit recognition for its role in the structure and function of individual marine benthic communities, and as a mechanism of autogenic and allochogenic changes in community composition. Generalizations drawn from modern environments may not be universally applicable to the fossil record though, since biologic influences on feedback have surely not remained constant through the Phanerozoic. For example, the diversity and abundance of nektonic macroinvertebrates contributing to sediment shelliness have declined greatly since the Mesozoic, as have the stalked echinoderms that served as important sources and stabilizers of shelly substrata in many Paleozoic and Mesozoic skeletal buildups. Large soft-substratum epifauna such as characterized Paleozoic and Mesozoic mid- to outer-shelf settings offered opportunities for taphonomic feedback lacking in comparable modern environments (see Jablonski and Bottjer, this volume). Furthermore, bioturbation rates and intensities have apparently changed throughout the Phanerozoic (Thayer, 1978; Larson and Rhoads, this volume), thereby affecting the concentration and burial of dead shell material. Our model, which has a physical, sedimentologic basis and incorporates present-day patterns of hardpart production and residence times, provides a null hypothesis against which to compare possible evolutionary changes in the role of taphonomic feedback in benthic communities.

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