2.4 Taphonomic Feedback (Live/Dead Interactions) in the Genesis of Bioclastic Beds: Keys to Reconstructing Sedimentary Dynamics

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1 Introduction

Densely fossiliferous beds – known variously as coquinas, lumachelles, and bioclastic limestones – are common features in marine sedimentary records and can have relatively straightforward post-mortem histories. Some of these concentrations form rapidly (e.g., most physical and biogenic event-concentrations; Fig. 1) whereas others accumulate over longer periods (hiatal concentrations; Fig. 5). Concentrated shells may be indigenous or exotic to the accumulation site, and may accumulate on the seafloor, below the seafloor, or undergo multiple episodes of burial and exhumation. Notwithstanding these variations, most skeletal material accumulates in biotic environments where living organisms both influence and can be influenced by the accumulating death assemblage (Fig. 2).

The influence of hardparts upon the ecological success of living benthos was termed taphonomic feedback by Kidwell and Jablonski (1983), who focused on live/dead interactions as a driving mechanism for benthic community change. Skeletal material provides islands of hard substrata in otherwise soft-bottom habitats and, where hardparts accumulate in abundance, can transform the seafloor into a coarser, firmer, and topographically more complex benthic habitat. The development of shell-gravel conditions, whether achieved instantaneously or gradually by autogenic or allogenic mechanisms, should facilitate colonization and reproductive success by species that require or prefer these conditions – predominantly epibenthic suspension feeders – and at the same time inhibit earlier species that can tolerate only the initial soft-bottom conditions (Fig. 3). Natural history observations and manipulative experiments provide abundant evidence for the importance of dead shells in structuring Recent benthic communities: dead shells provide domiciles, shelters from physical stress, spatial refuges from predators and competitors, substrata for attachment of eggcases, larvae, and adults, and generally create a heterogeneous habitat that favors higher species diversities of shelled benthos. Where they accumulate in abundance, dead shells also reduce the penetrability of sediments to burrowers and reduce the efficiency of both deposit- and suspension-feeding by infauna, all acting to reduce infaunal survivorship (see reviews by Kidwell and Jablonski 1983; Kidwell 1986b).

Changes in the structure and dynamics of benthic communities, whether driven by taphonomic feedback or by other biotic and abiotic processes, have in turn their own feedback upon the taphonomy of fossil assemblages. New species contribute new kinds or proportions of skeletal elements and also can directly enhance or reduce the preservation potential of bioclasts produced by other organisms (Fig. 2). This chapter focuses on the taphonomic aspects of live/dead interactions, and in particular the ways in which paleoecological, taphonomic, and other evidence can be used to reconstruct the short-term dynamics of sediment accumulation in aerobic marine environments. Pathways of taphonomic feedback and their outcome have undoubtedly shifted over the course of Phanerozoic evolution. This history has not been

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Fig. 1. Event-concentrations of bioclasts form rapidly relative to geological and ecological time-scales. Physical agents of concentration include storm surges, fairweather reworking, and turbidity currents; biological agents include predators, scavengers, biodevacting and burrow-lining infauna, and gregarious behavior of the bioclast-producing taxa themselves.

Fig. 2. Major pathways by which death assemblages are both influenced by and directly influence live benthos.
investigated systematically but clearly has implications both for paleoecology and for process-level studies of stratification.

2 Taphonomic Consequences of Live/Dead Interactions

Many live/dead interactions reflect active selection of dead shells by organisms for specific ecological ends. Very few of these appear to be obligate relationships driven by co-evolution (but see case of deep-sea limpets that graze exclusively on squid beaks, fish bones, or whale bones; Hickman 1983; Marshall 1987). Instead, shell-utilizing organisms are fairly opportunistic within certain limits, seeking out the most desirable of the readily available death assemblage. For example, hermit crabs (pagurids) and octopods will occupy a range of gastropod shell types, although their populations can be limited by the number of available shells (Mather 1982a,b; McLean 1983; McClintock 1985). The gastropod Xenophora, which attaches dead shells onto its own, accepts many kinds of small bivalves for camouflage when young but later prefers elongate shells (high-spired gastropods, scaphopods) presumably as stills to distribute its weight (Linsley and Yochelson 1973). Many encrusting organisms select substrata by size and/or hydraulic stability and thus do not necessarily prefer shells over lithic gravel, but in other instances ornamented or strongly concave shells are highly advantageous refuges from rasper predators (Bishop 1988; summarized in Kidwell and Jablonski 1983).

Other live/dead interactions are better characterized as unintentional. These include dead shells crushed by bottom-feeding rays, shells buried or exhumed by bioadvection, shell breakage and reorientation below the seafloor by bulldozing organisms, and disarticulation by scavengers. A complete gradation exists between such chance live/dead interactions and those known to be intentional.

All types of live/dead interactions provide information on the behavior and ecological strategies of benthos and all influence patterns of bioclastic accumulation. Some of these interactions such as heavy entanglement (e.g., Balson and Taylor 1982) increase the likelihood that the dead "host" is preserved and thus favor bioclastic accumulation, whereas other interactions are detrimental (e.g., shell attack by bioeroders, delayed burial by pagurids, bulldozing, and exhumation). Still other interactions, such as the preferential colonization of shell gravel by free-living macrobenthos, have few direct consequences for preservation of bioclasts but contribute new shells to the accumulating death assemblage. In this way they can have a strong additive effect on the formation of bioclastic beds.

2.1 Additive Effects

Preferential colonization by shelled benthos of isolated shells on otherwise disadvantageous soft or oxygen-poor seafloors is the first stage in development of many biostromal and biothermal deposits. Initial colonists can be endo- or epi-bysate forms that require only a small shell or shell fragment for attachment when juveniles, but then outgrow the need for such "life preservers" because of snowshoe and various isostatic adaptations when adults (e.g., anomiid bivalves, strophomenid brachiopods; various oysters, see Seilacher et al. 1985a). These colonists in turn provide substrata for colonization by con-specifics and others both while alive and after death. Many shell gruels thus can be "seeded" by death assemblages of deposit-feeders and small infaunal suspension feeders whose dead shells are small and widely dispersed. Lithic pebbles can serve the same function, but these are typically more scarce than indigenous shell debris in soft, level-bottom settings.

Once an initial, local concentration of shell material is formed, live/dead interactions can play a major role in further bioclastic accumulation. The epibenthic suspension feeders that require or prefer surficial shell-gravel conditions (i.e., firm to hard substrata) range in size but include larger-bodied species that contribute more skeletal carbonate per individual death. Shell production is further augmented when these shell-utilizing colonists are particularly fecund (as with true oysters) and/or highly gregarious. Sessile and attached epibenthos in particular are highly susceptible to death by burial because they are unable to escape even thin layers of fine sediment (although many have the ability to sweep themselves clean of small amounts of debris, and others can wait out temporary burial by slowing metabolism). Such obtrusion-related mortality can greatly augment bioclastic accumulation if depositional increments (1) are removed after death to allow for re-colonization of the "new" death assemblage and (2) are sufficiently infrequent that the second generation of colonists can grow to a threshold size and thereby survive the post-mortem rigors of the next cycle of burial, exhumation, and re-colonization. In this way some sedimentary dynamics should pump up bioclastic production and accumulation on and just below the seafloor.
In addition to facilitating colonization by new, more productive species, local concentrations of shell can trap skeletal debris in motion across the seafloor. Thickets of ramose corals and bryozoan colonies, for example, commonly initiate on dead shell substrata, behave in this way on both Recent and ancient level-bottom seafloors (Nelson et al. 1988; Cuffey 1985). The accumulated allochthonous debris, along with bioclasts produced by the local community, serves to further enlarge the initial concentration by providing an ever-widening halo of appropriate substrata for colonization.

Individually, epibenthic hardparts commonly have higher preservation potential by virtue of their size and (for some groups) calcitic mineralogies, but once accumulated to some threshold abundance they can have further beneficial effects on preservation. Close-spaced bioclasts reduce the erodibility of the seafloor owing to their relatively large size and tendency to interlock, and thus should protect underlying bioclasts from damage they might accrue from further burial-exhumation cycles. Also, by creating a less penetrable substratum for infauna (e.g., Newell and Hidu 1982), bioclasts should reduce sediment irrigation by bioturbators and thus allow favorable alkalinity to build up in porewaters. In situations where the bioclastic sediment is highly porous and contains little fine-grained matrix, bioclastic fabrics can foster free exchange with overlying waters, which are usually saturated or undersaturated with respect to calcium carbonate. Under these conditions of surficial exposure, shells are afforded little protection from boring organisms but should not experience true dissolution.

Live/dead interactions can figure in the genesis of bioclastic beds even when bioclastic accumulation occurs primarily beneath the seafloor surface. Unless buried very deeply (i.e., greater than the burrowing depth of common shelled infauna, ~20 cm), subsurface shell concentrations created by storms and bioadvection (Fig. 1) can impinge on benthic ecology by restricting infauna from burrowing to optimal depths. Such individuals are subject to higher metabolic stress from physical environmental fluctuations and/or higher rates of predation and other interference competition, thereby reducing survivorship (Pearce 1965; Haddon et al. 1987; Zwarts and Wanink 1989). Through the in-situ accumulation of infaunal hardparts (assuming that hardpart production exceeds hardpart destruction), the surficial sedimentary layer can become increasing shell-rich, reducing infaunal habitat space. In an idealized sequence (Fig. 3), deep-burrowing infauna and large-bodied mobile infauna become less abundant in favor of shallow-burrowing and smaller-bodied mobile infauna and, when shell-gravel conditions at or just below the seafloor are fully developed, eventually yield to dominance by taxa that tolerate or prefer a nestling or epifaunal habit.

### 2.2 Subtractive Effects

From the perspective of bioclastic accumulation, bioerosion is probably the most detrimental of live/dead interactions in that it both weakens and reduces hardparts to fine sediment (Highsmith 1981). This category includes surface rasping by grazing organisms, micro- and macroscopic boring, pitting and other shell damage by encrusters, and fragmentation by organisms that prey upon post-mortem encrusters and borers. Shell destruction rates can be very high in shallow-water tropical settings [e.g., >8000 g/m²/a by the sponge Cliona (Acker and Risk 1985), 40–168 g/m²/a for parrotfish (Frydl and Stearn 1978), 80–325 g/m²/a for echinoids (Russo 1980)]; infestation by borers is high even in temperate and high-latitude shell gravels (Young and Nelson 1988). Shell destruction by bioerosion is primarily a function of shell exposure on the seafloor — burial usually affords good if not complete protection — and is greater in shallow (photic) than in deep waters (Budd and Perkins 1980; Akpan and Farrow 1985). Evidence of boring and encrustation thus generally provides good evidence for delayed burial (and for exhumation of infauna).

Bioturbation has a range of effects: both burial (Meldahl 1987, references cited therein) and exhumation (McCave 1988), concentration (op. cit.) and dispersion have been attributed to mobile infauna, as have disarticulation, reorientation and fragmentation (Brett and Baird 1966a). Any of these processes that reduce the post-mortem survival of individual hardparts or interfere with the formation and survival of hardpart aggregations are detrimental to the development of bioclastic beds. By loosening and irrigating sediment, bioturbation also interferes with colonization by many shelled benthos, particularly suspension-feeding epibenthos, and reduces their preservation potential by maintaining undersaturated porewater conditions in the bioturbated interval. The typically aragonitic compositions and thin-shelled morphologies of species that characterize soft, shell-poor substrata predispose them to early physical and diagenetic destruction.

These kinds of interactions, not all of which are direct or selective interactions between live and dead individuals, act to keep initially shell-poor substrata in a shell-poor condition or to deplete them further. Once a local concentration of shells is formed, however, various kinds of biological, physical, and geochemical feedbacks should tend to enhance the preservation potential and can even favor growth of the bioclastic bed: shell-rich substrata stay rich or become even richer (Kidwell 1986a, 1989). It is unclear what minimum, threshold shell-richness is necessary to ensure (or at least significantly improve the probability of) bioclast preservation, but it is clearly an unstable equilibrium point determined by local taphonomic and ecologic conditions. In reef communities, for example, Highsmith (1980) and Hallock (1988) related bioerosion and thus accumulation potential to nutrient levels in the overlying water: as nutrient level increases, coral growth and recruitment decrease, carbonate production decreases, algal growth increases, and bioerosion intensity increases, thereby reducing the likelihood of a good fossil record.

### 3 Reconstruction of Sedimentary Dynamics

Patterns of small-scale erosion, deposition, and transport on the seafloor can be inferred from the extent and selectivity to which encrusting, boring, and other attaching organisms utilize individual shells. All of these interactions indicate shell exposure at or near the seafloor for some ecologically significant period of time: shell-utilizers must discover, colonize, and grow to a preservable size if exposure is to be taphonomically detectable. Strong correlations between sediment shelliness and
taxonomic composition are also consistent with taphonomic feedback on omission surfaces and within slowly aggrading shell gravels (hiatal accumulations). By using these and other ecologic, taphonomic, sedimentologic, and micro-stratigraphic lines of evidence, a high degree of detail regarding the dynamics of stratification can be achieved for bioclastic units.

### 3.1 Post-Event Colonization (Allogenic Taphonomic Feedback)

Event-concentrations, whether physical or biogenic in origin (Fig. 1), can be composed of (par)autochthonous (= indigenous pre-event community), allochthonous (*syn-event* transported shells), or mixed-origin death assemblages. Any of these types of background assemblage can evoke an ecological response from living benthos if the shells are exposed on the seafloor for an ecologically significant period of time, or if the shells occur in sufficient abundance within the sediment to alter its mass properties. The new assemblage produced by the post-event colonizers can be either admixed with or superposed upon shells of the original event-concentration.

The nature and extent of interactions between living benthos and dead shells depend upon burial pattems: post-event burial of the initial shell concentration can be immediate or delayed, permanent or temporary, deep or shallow (= thick vs. thin burial increments) (Fig. 4).

![BURIAL OF EVENT-CONCENTRATIONS Diagram](image)

**Fig. 4.** Live/dead interactions modify the ecologic composition and taphonomic features of simple event-concentrations to varying degrees depending upon the immediacy, permanence, and thickness of post-event burial by sediment. See text for explanation of each contingency.

#### 3.1.1 Immediate Burial (Including Obtrusion)

Immediate and permanent burial is essential for good preservation of articulated and/or lightly skeletonized specimens in the pre-event community. The thicker the layer of entombing sediment (=burial increment), the less likely that the burial-censused assemblage will be modified taphonomically or that some portion of the living fauna will escape. Bioclastic beds formed in this way offer minimal opportunities for taphonomic feedback because dead shells are sequestered from all but the deepest-burrowing infauna. The faunal assemblages of such concentrations should also have suffered negligible post-mortem damage from seafloor exposure.

When the burial increment is thin relative to typical burrowing depths of infauna and benthic scavengers, and the event-concentration itself is also thin, bioturbators may reorient, disarticulate, and even disperse shells out of the concentration. Alternatively, shells may be concentrated more tightly by *conveyor-belt* biogenic reworking of the burial increment (cf. Meldahl 1987). The fossil assemblage will otherwise resemble that of the deep-burial scenario, since the concentrated assemblage is never exposed at or sufficiently near the seafloor surface for infestation by encrusters and bioeroders. The background assemblage, however, may be augmented by endo-bysasset species that can penetrate the burial-increment and use dead shells for attachment (e.g., pinnid and some mytilid bivalves). These post-event fauna in turn can provide substrata for attachment by epifauna (either a live/live or live/dead interaction).

If burial is only temporary, geologically speaking – that is, the entombing sediments are removed by winnowing or reworking – shells produced by colonists of the burial increment can be amalgamated with the original event-concentration of shells. The thickness of sediment available should determine the kind of species that dominate the burial increment – thick increments will be characterized by soft-bottom shallow- and deep-burrowing infauna, whereas thin increments will be characterized by shallow burrowers and endo-bysasset forms – so that knowledge of the typical burrowing depths of exhumed species allows the original thickness of the burial increment and depth of its reworking to be estimated (Kidwell and Aigner 1985; Beckvar and Kidwell 1988; Kondo 1989). If the entire burial increment is removed during reworking, the original event-concentration may act as a "reference horizon" (sensu Seilacher 1985) for further bioclastic accumulation. Minor scour surfaces, pods of unworked sediment from the burial increment, and even laterally continuous remnants of the burial increment can remain to mark this second reworking event. These microstratigraphic features allow the background and post-burial assemblages to be distinguished, as they might otherwise resemble each other in ecology and taphonomy. If the original event-concentration is not resistant to erosional reworking, its assemblage can be completely admixed with its burial assemblage into a single graded bioclastic bed.

Ecologically, immediate burial of event-concentrations maintains continuous soft-bottom, shell-poor conditions on the seafloor. Taphonomic damage from "intentional" live/dead interactions will thus be relatively slight – few shells are available for living organisms to interact with – and will accrue largely from incidental interactions (e.g., damage from bioturbators) and from porewater-related processes...
mixing of ecologically unrelated faunas (owing to winnowing of death assemblages from temporary burial increments).

3.1.3 Other Situations

In high-stress environments, where salinity or oxygenation extremes restrict benthos, the taphonomy of bioclastic beds is less dependent upon the dynamics of sedimentation. Skeletal concentrations in such settings are typified by quiet-water biotal accumulations of nekton/plankton, opportunistic benthic colonizations, and rare high-energy event-concentrations that inject allochthonous shells. Skeletal concentrations from the Solnhofen Limestone, Posidonienschiefer, and other fossil-lagerstätten (Seilacher et al. 1985b, Brett and Seilacher Chap. 2.5, this Vol.), for example, differ significantly from bioclastic beds in fully aerobic environments, and this testifies to the significant taphonomic impact that living organisms can have upon the accumulation of dead shells.

Burial of event-concentrations by coarse, relatively porous sediment (e.g., sand, gravel, shell debris) is less effective than fine-grained sediment in smothering fauna and excluding fouling organisms. Many encrusters in fact prefer the cryptic habitats provided by the under-sides of shells because of less intense predation, and thus avoid the seafloor surface sensu stricto. Scoffin and Henry (1984) found that encrusting scleropods can survive at least several months of burial under 1-2 m of hurricane-deposited rubble on Jamaican reefs, whereas burial under only a few cm of mud (silt-clay mixture) is generally lethal for suspension feeders. The relative sensitivity of bivalves to various thicknesses and grain sizes of anastrophic burial has been examined in considerable detail by Kranz (1974) and others. The minimum effective thickness of burial increments thus varies significantly among sediment types and must be considered in reconstructing the dynamics of interstratified bioclastics.

3.2 Autogenic Taphonomic Feedback

Hypothetically at least, live/dead interactions can figure in the formation of bioclastic beds even without the "seed" of an initial event-concentration and also in the absence of other reworking events. Given early diagenetic regimes that allow for net accumulation of some of the local death assemblage, repeated colonization of a non-aggrading seafloor should gradually transform the initially shell-poor soft-bottom habitat into a more shell-rich and thus coarser, firmer, and eventually topographically complex habitat (Kidwell and Jablonski 1983) (Fig. 3).

This autogenic mode of shell-gravel genesis results in ecologically mixed faunal assemblages because later shell-tolerant taxa occupy the same sedimentary volume as the initial soft-bottom forms. Vertical mixing by bioturbators or by physical reworking would further homogenize the assemblage, obliterating any microstratigraphy produced by the progressively more epifaunal habit of successive colonists. The resulting bioclastic unit will lack the minor scour surfaces and winnowed
interbeds that characterize accumulations produced by burial/exhumation cycles (Sect. 3.1. above). Post-mortem infestation will vary: bioclasts produced by the initial soft-bottom community (particularly by the deepest-burrowing taxa) can remain buried for the duration of autogenic feedback and thus can show negligible damage from shell-utilizers, whereas bioclasts produced by later, more surficial shell-gravel dwellers will have suffered proportionately greater taphonomic damage.

The diffuse, interference competition represented by autogenic taphonomic feedback is difficult to demonstrate unambiguously in the fossil record, unlike the direct evidence provided by most live/dead interactions at the individual level (e.g., post-mortem boring, encrusting, and hermiting of shells; Walker 1988). Autogenic feedback is certainly consistent with the well-documented behaviors of Recent benthos in the presence of dead shells (see Sect. 2 and references therein), but such analogies are not necessarily appropriate for much of the fossil record.

If taphonomic feedback plays an important role in shaping benthic communities (and thus bioclastic beds), then strata containing greater densities of shell should also contain assemblages with greater relative abundances of shell-gravel species. This can be tested statistically with the null hypothesis being one of no correlation (Kidwell 1986b), implying that dead hardparts played no role in shaping the living community. Some insight into the life habits and ecological preferences of species is essential for such an analysis. In addition, alternative explanations for a correlation between fauna and sediment-shelliness, such as differences in water energy or selective diagenesis, must be accommodated or rejected if the taphonomic feedback explanation is to be accepted.

### 3.3 Multiple-Event (Hiatal) Accumulations

Many bioclastic accumulations are longer-term buildups that comprise many event-scale concentrations. The subsidiary event-concentrations can be of any type or combination of types described above (Sects. 3.1. and 3.2.). If simply amalgamated, they yield a microstratigraphically complex bioclastic deposit that can include shell-poor intercalations (Fig. 5). Alternatively, hiatal accumulations can comprise little or no internal stratigraphy if (1) physical and biogenic reworking were intense during buildup or (2) shell-gravel conditions went virtually uninterrupted by burial/exhumation cycles. This latter situation results in interlocking bioclastic fabrics and, in some cases, significant boundstone/ framstone increments. In all poorly stratified hiatal accumulations, taphonomic and ecological evidence becomes even more valuable for reconstructing event-scale sediment dynamics.

The term *hiatal* refers to (1) the close association of many of these bioclastic accumulations with discontinuity (hiatal) surfaces (see Kidwell Chap. 6.3, this Vol.), (2) their composite, multiple-event nature and inclusion of many minor discontinuities as opposed to simple event concentrations, and (3) their formation during significant slowdowns if not complete hiatuses in the accumulation of nonbioclastic sediment (e.g., siliciclastics, carbonate mud, other allochems) owing to negligible supply, continuous transport, or active removal of such sediment. Many are characterized by some form of faunal condensation sensu Frütsch (1978), and some are stratigraphically condensed sensu stricto, that is, thin relative to coeval strata elsewhere (see Kidwell Chap. 6.3, this Vol., for review and examples). Hiatal accumulations are not necessarily condensed, however, because bioclasts can accumulate in significant thicknesses that equal or even exceed aggradation in adjacent environments. Biothermal and bioclastic shoals are common examples of stratigraphically normal or even expanded shell-rich records. (See note added in proof.)

The three basic pathways of hiatal accumulation characterized in Fig. 5 have been described in greater detail elsewhere (Kidwell and Jablonski 1983; Kidwell and Aigner 1985; Kidwell and Aigner 1989) and are idealized types: all intergradations are possible (examples in Beckvar and Kidwell 1988). These models were developed for siliciclastic and mixed siliciclastic-carbonate systems, but can be adjusted for purely carbonate systems as well.

#### 3.3.1 Continuous Omission of Nonbioclastic Sediment

Under conditions of sediment starvation or complete bypassing of sediment in suspension, shell gravel conditions can be maintained continuously on the seafloor by local bentic production (± addition of allochthonous shells) (Fig. 5a). Faunal
assemblages should be dominated by shell-gravel dwellers, most notably epibenthos (both free-living and attached), nestlers, and shallow-burrowing taxa that are either tolerant of a semi-infaunal habit or capable of exploiting matrix available between bioclasts. Bioclasts should exhibit a relatively high frequency and intensity of infestation by boring and encrusting organisms, a high proportion of disarticulated elements, and a large proportion of fragments (fragmentation can be biogenic or physical and pre- or post-depositional in origin and thus is a poor environmental indicator). Water depths can be inferred from the composition of borers and encrusters and from surface features of individual shells; abraded fragments for example indicate repeated shifting of shells and sediment on the seafloor, consistent with shallow water (unless allochthonous, of course). Age-at-death of autochthonous epibenthos provide a maximum estimate for rates of seafloor aggradation.

3.3.2 Episodic Deposition and Omission

Stepped aggradation of the seafloor repeatedly renews soft-bottom habitats, which through autogenic taphonomic feedback (~allochthonous shell input) become increasingly shell-rich during intervening periods of non-aggradation (Fig. 5b). Shell enrichment by taphonomic feedback will be largely limited to the upper 10–20 cm of any depositional increment, although the seafloor may then aggrade upward by shell accumulation once a predominantly epibenthic shell-gravel community is established. Complex accumulations formed by repeated cycles of deposition/omission thus can include some relatively shell-poor layers if depositional increments are thick. Faunal assemblages will range from soft-bottom dominated (shell-poor layers) to ecologically mixed (shell-rich, upper part of original depositional increments) and shell-gravel dominated (shell-rich builds up above each depositional increment).

Although depositional increments can be intensely bioturbated, at least before shell abundance becomes prohibitive, they are not disturbed by physical reworking; moreover, each increment and its living benthos eventually undergoes permanent (rather than temporary) burial. Consequently, a significant number of specimens (from early and from latest colonists) can be preserved articulated and even in life positions. Shell damage by endo- and epibionts will be variable, with early deep-burrowing colonists bearing lighter infestations than later colonists. Fragmentation can be extensive throughout each increment and will affect all ecological groups, although shell-gravel taxa may suffer disproportionately because of the combined effects of physical and biological processes. The sedimentary matrix in the upper part of each increment may be winnowed.

3.3.3 Episodic Deposition and Erosion ± Omission

Alternating deposition and erosion amalgamates event-concentrations such as described individually in Section 3.1. Once bioclastic material has accumulated to an erosionally resistant threshold thickness, a microstratigraphic record of the discrete event-concentrations can be preserved. The type and extent of taphonomic feedback in these kinds of hiatus accumulations depends upon the length of delay between erosional reworking — which concentrates soft-bottom taxa into a shell-gravel lag — and burial under the next depositional increment. Thus the faunal composition of the complex accumulation can be (1) dominated by well-preserved but reoriented soft-bottom taxa (ecologically insignificant delay in burial) or (2) a mixture of soft-bottom and shell-gravel taxa, both sets having accrued considerable taphonomic damage. All specimens from the reworked increments will be reoriented ± disarticulation; soft-bottom infauna that remain in life position indicate the maximum depth of erosional reworking of the substratum. Infauna preserved in life positions within shell-rich parts of the accumulation should be suspected of being shell-gravel dwellers; such occurrences provide more dependable insights into the ecological tolerances of fossil species than inferences based on the ecology of modern representatives.

Such sawtooth histories of alternating deposition and erosion are most common in shallow marine settings, and are usually characterized by winnowed sedimentary matrices and many minor discontinuity surfaces produced by scour and firmground development. Depending upon the depth of erosional reworking, depositional increments may be only partially truncated, leaving intercalations of less shelly, less winnowed, and less modified substratum within the complex accumulation. These layers and pods provide a useful baseline for background conditions, which have lower preservation potential than the higher energy concentration events.

4 Summary and Conclusions

Live/dead interactions are pervasive in aerobic benthic habitats and can have significant consequences for bioclastic deposits. Organisms with mineralized hardparts contribute bioclasts whose accumulation modifies the physical habitat, facilitating species that tolerate or prefer shell-rich substrata, and inhibiting the success of earlier soft-bottom colonists. New epibenthic colonists commonly produce more skeletal carbonate than precursor benthos, whereas other shell-utilizing colonists destroy or inhibit further accumulation of shell material. The budget of shell production versus destruction by live individuals is not known quantitatively for any environment, but live/dead interactions clearly have both additive and subtractive aspects.

Most bioclastic beds, even many event-concentrations, consequently have complex taphonomic and paleoecologic histories related to the accumulation of shells on or near the seafloor. Together with conventional sedimentologic and microstratigraphic criteria, taphonomic and paleoecologic features can be used to reconstruct detailed, process-level histories of aggradation, erosion, and omission/transport on the seafloor. Post-mortem biocorrosion and encrusting indicate exhumation and seafloor exposure of some duration; the burrowing depth of exhumed infauna indicates minimum depths of erosional reworking; age structure of post-event colonists indicates minimum duration of seafloor exposure; distinctive sedimentary fill of skeletal cavities records depositional increments not otherwise preserved; and quality of fossil preservation in the uppermost parts of bioclastic deposits reveals the immediacy, permanence, and thickness of burial deposits.
Given sweeping evolutionary changes in the diversity of species that produce, utilize, and destroy bioclasts, it would be surprising if patterns of bioclastic accumulation did not change over Phanerozoic time. The past 600 million years have seen an increase in the body size and robustness of shelled benthos and progressive infaunalization, both favoring skeletal accumulation. This has been countered by an overall shift from calcite to less stable aragonite hardparts, an increase in duraphagous predators and bioeroders, decimation of large-shelled nekton, and an increase in the depth and/or intensity of bioturbation, all of which should reduce the likelihood of individual shells and shell concentrations being preserved (Kidwell 1990). Documentation of how pathways and mechanisms of taphonomic feedback have changed would be of value not only to the paleontologist concerned with fossil behavior and post-mortem bias, but also to the geologist concerned with extracting maximum paleoenvironmental information from sedimentary deposits. Evolutionary changes in the dynamics of bioclastic accumulation would admittedly complicate the straightforward application of actualistic models to reconstructing the past. On the other hand, such evolution might better explain secular trends in bioclastic stratification previously attributed to broad paleogeographic changes or to cumulative diagenesis.

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Note added in proof: See Kidwell (The Stratigraphy of Shell Concentrations, in Taphonomy: Releasing Information from the Fossil Record, P.A. Allison and D.E.G. Briggs, eds., 1991) for updated treatment of complex shell concentrations, and specifically the restriction of the term "bioturbate concentrations" to stratigraphically condensed shell accumulations. This usage supersedes that of this paper, which was last revised in May 1989.