

PHANEROZOIC EVOLUTION OF MACROINVERTEBRATE SHELL ACCUMULATIONS:
PRELIMINARY DATA FROM THE JURASSIC OF BRITAIN

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INTRODUCTION

Given sweeping evolutionary changes in the diversity and environmental deployment of species that produce shells, destroy shells, and otherwise interact with shells, it would be surprising if patterns of shell accumulation did not change over Phanerozoic time. Documentation of such patterns might indicate how and to what degree post-mortem bias has changed, and thus the taphonomic comparability of data sets used in paleobiologic modelling. At the same time, long-term patterns in shell accumulation can be products of evolutionary ecology, and thus represent an underexploited source of paleobiological insight themselves.

This paper outlines an analytical approach to identifying and interpreting long-term trends in hardpart accumulation in marine level-bottom settings, and presents preliminary results from a pilot study in the Jurassic of Great Britain.

NATURE OF THE PROBLEM

Phanerozoic trends in post-mortem shell accumulation are difficult to predict. On the one hand, increases in the diversity, body size and (perhaps) robustness of shelled benthos over the past 600 million years should favor increasingly thick, diverse, and numerous bioclastic accumulations, as should the progressive infaunalization of shelled benthos. With infaunalization, shells can accumulate within the sediment (infaunal death assemblages, plus shells piped into open burrows) as well as on the seafloor (epifaunal death assemblages, allochthonous hardparts), so that an accumulation can be three-dimensional from its inception. On the other hand, the shift from calcitic to aragonitic hardparts, increase in duraphagous predators and bioeroders, decimation of large shelled nekton, and possible increase in depth or intensity of bioturbation should all reduce the likelihood of individual shells and shell concentrations being preserved (Table 1). Only semi-quantitative information is available, at best, for any of these factors in the biostratigraphic equation.

Long-term trends in shell accumulation therefore must be determined empirically at this stage, using objectifiable features such as the dimensions, dense-packing, taxonomic composition, and other taphonomic attributes of individual bioclastic concentrations. Based on my own field observations (stressing Cenozoic deposits), impressions from the literature, and discussions with Paleozoic workers, my working hypothesis is that the record of marine level-bottom settings can be divided into two biostratigraphic styles or modes (Kidwell 1988a).

1. Archaic mode typifying Paleozoic and Triassic strata and characterized by thin (few 10's cm), relatively two-dimensional bioclastic concentrations which are dominated by brachiopods and other epifaunal and semi-infaunal taxa. The Devonian Hamilton Group (Parsons et al. 1988) and Triassic Muschelkalk (Aigner 1985) exemplify this mode

Table 1. Phanerozoic trends in factors that influence the post-mortem accumulation of shells.

	<u>Oppose Accumulation</u>	<u>Favor Accumulation</u>
Increase:	Bulldozers Bioeroders Sediment irrigation Aragonitic shells	Diversity & burrowing depth of shelled infauna Body sizes of shelled benthos Shell thickness
Decrease:	Large shelled nekton Shelled epifauna on soft substrata Calcitic shells	

in siliciclastic and mixed carbonate settings. Thick crinoidal calcarenites represent a major exception to the archaic pattern in Paleozoic-Triassic rocks, although it should be noted that these "rolling stone" shell gravels differ in many respects from "interlocking" shell gravels composed of non-spheroidal bioclasts.

2. Modern mode typifying Cretaceous and Cenozoic strata and characterized by thin pavements plus fully three-dimensional bioclastic concentrations (≥ 1 meter in thickness) which are dominated by mollusks and other epifaunal and fully infaunal taxa. Modern strata exhibit a broader range of sizes of shell concentrations (or larger proportion of thick concentrations) and a greater variety of ecological habits than archaic strata, and can be dominated by aragonitic, calcitic or a mixture of several mineralogies. This mode is exemplified by the siliciclastic to mixed carbonate Miocene Chesapeake Group (Kidwell 1982), Pliocene Imperial Formation (Kidwell 1988b), and Paleogene Aquia Formation (Ward 1985).

The 2-mode stereotype is not an arbitrary hypothesis -- it captures the biostratinomic gestalt of rocks I have seen -- but it is just one of many testable hypotheses. It may well be, for example, that the Phanerozoic is characterized by three biostratinomic styles that correspond to the Paleozoic, Mesozoic, and Cenozoic Eras or to Sepkoski's (1981) Cambrian, post-Cambrian Paleozoic, and Modern Faunas. Alternatively, the record may be characterized by an even larger number of styles, or by continuous directional change in style, or by no change. This last result -- no change over Phanerozoic time in the nature of bioclastic concentrations -- is counterintuitive and would be at least as interesting as any other result.

Thus for an unprejudiced test, data must be collected initially from all kinds of bioclastic deposits, regardless of inferred mode of formation, and taphonomic features must be treated as independent variables. Quantitative data on some features, such as dense-packing, disarticulation, and fragmentation, are difficult to acquire from the literature with consistency. Field verification of selected reports and the development of semi-quantitative categories for plotting data are required to integrate different sources and build an adequate dataset.

Any analysis of Phanerozoic changes in the nature of the fossil record must also take into account possible driving mechanisms and artefactual effects. A trend toward bigger and more complex shell accumulations, for example, could reflect evolutionary replacement by benthos that produce more shell material or whose shells are less susceptible to post-mortem destruction. It could also reflect the evolutionary or

ecological ascension of organisms that concentrate dead shell material, create conditions favoring shell preservation, or reduce the effectiveness of shell destroyers and dispersers.

Such a trend can also be an epiphenomenon of paleogeographic changes. Widespread epicontinental seas, with their distinctive conditions for shell production, preservation, and accumulation, virtually disappeared in the Cenozoic. Other tectonic settings have also waxed and waned along with supercontinent accretion and dispersion, so that it may be impossible to sample biostratinomic "evolution" independently of paleogeographic evolution. The pattern could also be to some degree an artefact of uneven sampling of lithofacies, in part imposed by paleogeography (e.g., Cenozoic under-representation of cratonic carbonates), or of less diagenesis in younger rocks. Biostratinomic data thus ideally must include information on the lithofacies, tectonics, and paleolatitude of individual shell concentrations so that these can be factored out of any long-term pattern.

BIOSTRATINOMIC PATTERNS IN THE BRITISH JURASSIC

The two-mode hypothesis suggests that the Jurassic could be a pivotal period in the history of shell accumulations, lying between the apparently archaic Triassic and the definitely modern Cretaceous records. The Jurassic might be characterized (1) by some intermediate condition, (2) by the intercalation of both archaic and modern style records, each linked to a particular lithofacies or taxonomic group, or (3) by largely archaic (or modern) deposits throughout.

A further incentive to focussing initial work on Jurassic strata is the abundance of both brachiopods and bivalves, which are major bioclastic components in Paleozoic and Cenozoic rocks respectively. Comparing brachiopod- and bivalve-dominated assemblages of identical rather than disparate ages provides a straightforward way to determine (1) the relative taphonomic susceptibilities of the two groups in the absence of actualistic data for brachiopods, and (2) the extent to which biostratinomic patterns are determined by hardpart producers as opposed to taphonomic environment (i.e., taxon- rather than age-dependent biostratinomic patterns).

The shallow-marine British succession is particularly advantageous for study in that it includes both condensed and expanded sections of siliciclastic and carbonate facies. The stratigraphy and paleontology of these strata are well-documented in a voluminous literature dating to William Smith. Many inland sections have disappeared owing to disuse of quarries, but classic exposures on the Dorset and North Yorkshire coasts are still highly accessible and allow field checking of published biostratinomic data.

By comparing shell concentrations in the same set of strata, biostratinomic variation imposed by physical environment and tectonic setting is minimized. Variation imposed by extrinsic biological factors, such as stage of evolution of bioeroders and shell-crushing predators, can also be minimized: shells of contemporaneous benthos, regardless of their susceptibility to post-mortem disintegration, must experience similar taphonomic pressures if they accumulate in the same environment during the same period of time. This approach should reveal the relative importance of processes and attributes inherent to the shell producers. Restated, if concentrations of dissimilar taxonomic composition differ biostratinomically, this must to some degree be a function of the ecology and output of benthic producers and the taphonomic susceptibility of their shells, rather than post-mortem conditions per se.

Table 2. Field-verified synonymy of bioclastic terms used in the British Jurassic literature. Minimum bioclast size = 2mm.

<u>Densely Packed Fabric</u>	<u>Loosely Packed Fabric</u>	<u>Dispersed Fabric</u>
shell-supported	nearly shell-supported	shells common
lumachelle	shells very abundant	shells abundant
bioclastic rudstone		biocl. floatstone
coquina	<u>Inconsistent Usage</u>	
"crowded with shells"	shell conglomerate	
"more shell than matrix"	ragstone (quarrymen's term)	

Preliminary data from the Jurassic of Great Britain (Figure 1) indicate in fact that shell concentrations of different taxonomic composition do differ significantly in the biostratigraphic features of (a) close-packing of shells and (b) total thickness of the concentration. A complete bibliography and locality index for these data will be published in a longer paper in preparation. Close-packing of shells was scored with respect to three categories: densely packed (shell-supported), loosely packed (only locally shell-supported; not obviously shell-supported but shells in close proximity, i.e. occurring within one shell diameter of each other), and dispersed (clearly matrix-supported; shells generally \gg 1 shell diameter apart). These semi-quantitative categories are synonymized with bioclastic terms encountered in the British Jurassic literature in Table 2; the synonymy was verified by field checks of selected outcrops. Although shell concentrations may well differentiate themselves with respect to state of preservation, size-sorting of shells, and other taphonomic features as well, these data proved virtually impossible to obtain consistently from the literature or with sufficient confidence.

Brachiopods. Throughout the Jurassic, brachiopod concentrations tend to be archaic in nature. They are typically small in scale (usually \leq 20 cm thick) and taphonomically simple, containing much larger proportions of unbroken and articulated specimens than bivalve-dominated and polytaxic concentrations (Figure 1). Well-known examples from England include the Aalenian Plectothyrus bed and the Bathonian Epithyrus beds and houeti bed. Some named beds, for example the famous Oxfordian Torquirhynchia inconstans bed at the base of the Kimmeridge Clay, are so sparsely fossiliferous as to not count as concentrations at all: these are brachiopod-bearing horizons rather than bioclastic deposits in the common sense of the word. Body sizes are typically small (\leq 4 cm).

Although brachiopod and bivalve distributions in the Jurassic were influenced by the fluctuating boundary of the Tethyan and Boreal realms, the pattern emerging from my limited British dataset is probably not a simple artefact of biogeography. In their reviews of brachiopod occurrences from both realms, both Ager (1965: 149) and Hallam (1972: 403, in re Hallam 1955; in litt. 1989) state that Jurassic brachiopod concentrations in general tend to be thin and localized.

Infaunal Bivalves and Associated Soft-Bottom Fauna. Accumulations of infaunal and semi-infaunal bivalves range from thin pavements and small nests of shells to thick, densely packed bioclastic accumulations that are completely modern in aspect (Figure 1). Well-known examples from England include the Basal Shell Bed and stratigraphically higher Roach of the Portland Limestone (each 2- to 3-m thick). The Pliensbachian Pecten seam of the Cleveland Ironstone, Pliensbachian Jamesoni Limestone, Bajocian biostromes of the Lincolnshire Limestone, and Oxfordian Mvophorella (trigoniid) beds of the Corallian Group are all 1-to 2m-thick units of intercalated densely and loosely

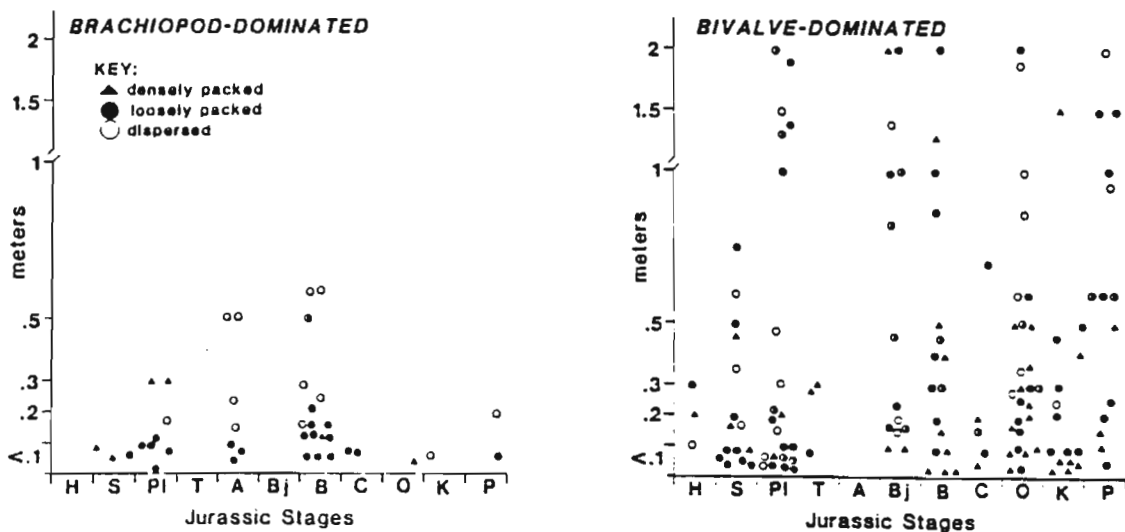


Figure 1. Brachiopod shell concentrations in the British Jurassic are almost exclusively thin accumulations (25 of the 28 sampled are ≤ 20 cm; excludes dispersed assemblages), whereas bivalve concentrations exhibit a broad range of thicknesses ($n = 112$ densely or loosely packed accumulations; excludes oyster concentrations). These and other data indicate strong phylogenetic as opposed to environmental control of the physical scale of bioclastic accumulations, and that the Jurassic is characterized by both archaic and modern styles of fossil record.

packed shell (dense-packed fabric predominates).

These accumulations commonly contain a complex microstratigraphy of subsidiary assemblages and shells in various states of post-mortem modification (reorientation, fragmentation, bioerosion, disarticulation). The co-occurrence of encrusting and epifaunal taxa (e.g. bryozoans, pectinids, *Ostreacea*) in small numbers may indicate taphonomic feedback within the benthic community. Originally aragonitic shells are preserved as moldic voids, recrystallized calcite, or geodal fills. Body sizes can be quite large (~6 cm for infauna, ~12 cm for pectinids, bivalve-like, and isognomonids).

Oysters. Like infaunal bivalves, oysters form a complete spectrum of shell accumulations, ranging from small clusters of mutually attached specimens in life positions and pavements of storm-scattered valves (e.g., various *Nanogyra* concentrations; Fürsich and Oschmann 1986) to thick densely packed accumulations created by repeated colonization and/or physical reworking. *Praexogyra hebridica* of the Fullers Earth Formation (Bathonian) forms some of the most impressive accumulations. For example at Langton Herring in Dorset this small species (~4 cm), which Hudson and Palmer (1976) describe as the first true *Ostreinae*, composes a 2+m-thick cross-bedded deposit. This deposit is extraordinarily similar in biostratigraphy to 1- to 6-m thick oyster coquinas of Pliocene age (Kidwell 1987). The Jurassic bioclastic units are not coherent bioherms but thinly stratified, densely packed accumulations of shell fragments and disarticulated and articulated specimens, most of which are unattached; shell sorting and orientation vary from layer to layer and, if analogy may be drawn with Pliocene examples, much of the shell material is parautochthonous to allochthonous in origin.

Data from bioclastic and 'reefoid' concentrations of *Ostreacea* (including *Grvphaea*,

concentrations. The sparsity of thick brachiopod concentrations that have been described in the literature should thus be meaningful. Increasing the sample size is, of course, desirable, but this is more likely to fill in the envelopes as already defined than to shift the overall patterns significantly.

One bias against thick concentrations is operational. Many thick bioclastic units -- certainly most concentrations that are thicker than 0.5m, and even some thinner concentrations -- are clearly amalgamations of many smaller-scale concentrations (i.e., multiple-event accumulations; microstratigraphically complex shell deposits). The small-scale components include shelly storm lags and layering imparted by repeated winnowing and benthic recolonization. In situations where amalgamation has been complete with no intercalations of less shelly sediment, there is little ambiguity: the uniformly bioclastic deposit is thick and is so scored in the diagram. Just as clearly, where intercalations of less shelly sediment are more numerous and thicker than intervening shell-rich layers, the stratigraphic interval should be scored as a series of discrete, thin shell concentrations. Intermediate conditions present a problem in categorization. If a truly objective dataset is to be compiled, we need a standard, scale-dependent procedure to score complex concentrations with respect to degree of amalgamation or homogeneity in close-packing. Until such a system is developed and widely applied, however, this information is extremely difficult and often impossible to extract from the literature. Most of the thickest concentrations plotted in Figure 1 were personally field-checked and categorized using my own system (Kidwell & Holland, in prep.); these scores are thus relatively consistent.

The thickness-frequency distributions for both brachiopod- and bivalve-dominated concentrations indicate that most are small in scale (≤ 20 cm thick) (Figure 1). Most data points for small-scale concentrations do not represent a particular individual shell concentration, but instead indicate a collection of similar shell concentrations from a local section. This is because literature sources generally do not stipulate how many shell plasters or nests occur but only that plasters and nests are present in a stratigraphic interval, and in fact such small-scale concentrations are often impractical to count. Data points for thicker shell concentrations on the other hand generally do represent a single, specific shell deposit. Small-scale concentrations are thus even more abundant relative to thick concentrations than is apparent in these two plots.

IMPLICATIONS FOR TAPHONOMY AND EVOLUTIONARY ECOLOGY

These preliminary data (Figure 1) are consistent with a two-mode Phanerozoic record, and suggest that the Jurassic record is biostratinomically mixed in nature. Although Jurassic bivalve communities were ecologically "archaic" like Paleozoic communities, containing far higher proportions of epifaunal species than Recent faunas (Hallam pers. comm. 1989 and ms in press), they were biostratinomically modern in aspect by the Jurassic: polytaxic, infauna-, and epifauna-dominated concentrations all span a range of dimensions. It appears that if bivalve concentrations ever were predominantly archaic in nature, it was sometime before the Jurassic. The timing of such a change-over bears investigation. In contrast, the brachiopod record was clearly archaic in the Jurassic. If brachiopods ever had the ecologic and taphonomic wherewithal to form dense, large-scale shell accumulations, they lost it by the mid-Mesozoic and did not regain it. Reports indicate that several early Paleozoic brachiopod groups in fact could form significant bioclastic concentrations up to 4.5 m in thickness, most notably the pentamerides, atrypids, and trimerellaceans (Johnson 1977; Johnson & Lescinsky 1986; Webby & Percival 1983; C. Bolton, T. deFreitas, E. Gosselin, T. Sami, pers. comms. 1988).

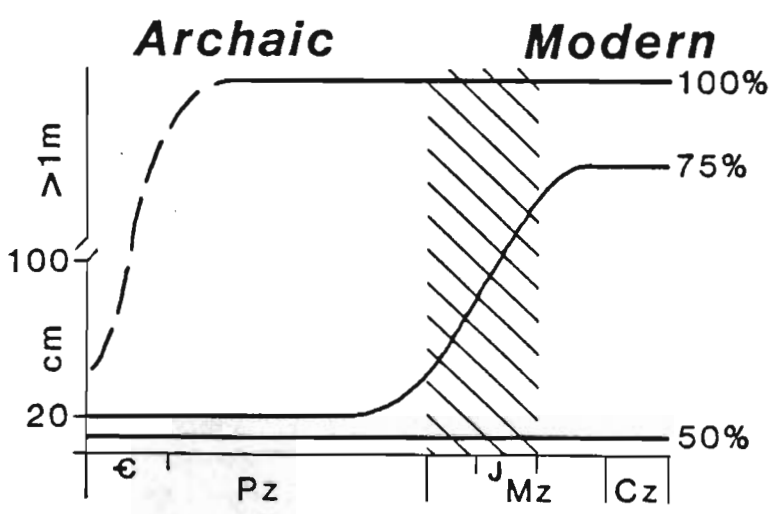


Figure 2. Working hypothesis for Phanerozoic trends: thick (>>20cm) shell accumulations are significantly more abundant in post-Paleozoic rocks; the early Mesozoic is a transitional interval that contains both biostratinomically archaic and modern facies. In the Paleozoic, exceptional "modern" accumulations are most often formed by crinoids, pentamerides, and trepostomes, whereas the major post-Paleozoic contributors to thick bioclastic concentrations are bivalves, gastropods, larger forams, barnacles, and cyclostome and cheilostome bryozoans. Because larger accumulations tend to have taphonomically and ecologically complex histories, this trend is symptomatic of evolution in the dynamics of benthic communities and of possible changes in the quality of the fossil record. Percent-abundance contours are estimated.

A shift in patterns of skeletal accumulation may also appear in other long-ranging groups such as gastropods and cyclostome bryozoans which seem to rarely dominate significant bioclastic accumulations before the Jurassic. Shell-gravel formers that originated or first diversified in the post-Paleozoic, such as calcified barnacles and coralline algae, would also contribute to an apparent long-term change in bioclastic deposits. The corallines (calcareous red algae) are a particularly interesting example because they appear to have benefited from intensified herbivory in the late Mesozoic (Steneck 1983), whereas this interfered with the survival (ecologic and taphonomic) of other benthos on photic-zone seafloors. Larger forams are sporadic but locally significant contributors to the pattern: except for the late Paleozoic fusulinds, most of these giants have been mid-Mesozoic and younger in age (e.g. orbitolinids, alveolinids, various rotalaceans including nummulitids; Brasier 1980, 1988). Intuitively, it seems that clypeasteroid and spatangoid echinoids should form major bioclastic units, but they appear to be limited to comparatively thin coquinas ("sand dollar lumachelles") and dispersed fabrics in my experience. As with the brachiopods, some lineages of crinoids formed significant concentrations in the Paleozoic, but this mode does not reappear among locally abundant -- but low diversity -- post-Paleozoic representatives.

The long-term shift toward bigger, denser(?), and taphonomically and ecologically more complex shell accumulations (Figure 2) -- if it stands up to further testing -- contradicts expectations based on evolutionary trends in organisms that destroy and otherwise interact with dead shell material (factors in Table 1). Bioeroders of all sorts diversify taxonomically, ecologically, and paleoenvironmentally in the post-Paleozoic, as do shell-dispersing and sediment-irrigating bioturbators; shell-crushing predators and scavengers radiate, large-bodied epifauna and shelled nekton decline, and infaunal but aragonitic-shelled bivalves dominate a broader spectrum of habitats. If this list is taken

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at face value, "life after death" should have become tougher over the course of the Phanerozoic -- the survival of individual shells and shell concentrations should have become more tenuous and less likely. Instead, it appears that stratigraphically significant post-mortem accumulations of shells are at least as abundant and probably more abundant in the younger record than in the older, and that over time their taxonomic and ecological diversity increases as well. This pattern is unlikely to be an artefact of diagenesis or uneven sampling of facies, inasmuch as significant skeletal accumulations are known from Paleozoic rocks and from a spectrum of level-bottom settings.

The Jurassic represents approximately 70 m.y. -- less than 10% of Phanerozoic time -- and thus data from this one period, however pivotal, and from one small area (Great Britain) proves little about Phanerozoic trends [although Hallam in litt. 1989 confirms that the data are characteristic of the global Jurassic picture]. Clearly, clades of shell-gravel-producing taxa need to be traced back in time with broader geographic coverage. This pilot study has nonetheless clarified in my own mind the nature of the analytic problem, and has made me reconsider some factors that I had initially thought might drive Phanerozoic changes.

Of these factors, externally imposed taphonomic pressures are not predominant, in fact shells accumulate despite what should be increasingly aggressive post-mortem conditions. Examining the Jurassic data in particular: taxonomically disparate concentrations, formed during the same stage in the evolution of taphonomic agents, are nonetheless biostratigraphically distinct (Figure 1). The taphonomic environment thus does not appear to impose a ceiling on bioclastic accumulations at this time, making it even less likely that the general post-Triassic increase in shell gravels is attributable to "taphonomic release" by shell destroying and dispersing organisms.

Instead, the formation of significant bioclastic accumulations follows phylogenetic lines among shell-producers. These are not immediately predictable: some taxa become major contributors to shell gravels whereas others never do, even though they share taphonomically and ecologically advantageous characteristics. Life habit, for example, does not appear to be a major factor in itself: modern shell gravels can be composed of infaunal, semi-infaunal, free-living or attached epifauna. Body size or robustness of skeletal hardparts similarly does not play an important or pivotal role: small-bodied Praexogyra forms major accumulations whereas large-bodied Gryphaea generally does not; delicate cheilostomes and cyclostomes can dominate shell gravels as can robust trepostomes. Mineralogy is not a primary determinant: post-Jurassic shell gravels can be dominated by aragonitic, calcitic, bimineralic, or a mixture of shell types. Gregarious behavior, either as larvae or adults, does not emerge as a major factor: innumerable "nests" of size-sorted, life-position Jurassic terebratulids and rhyconellids suggest that these organisms lived in groups on the seafloor, possibly attaching to each other, and yet these conclaves amounted to little, bioclastically speaking, compared to similarly gregarious oysters, scallops and turritellids.

The more important attributes appear to be (1) post-mortem durability as determined by the microarchitecture and organic matrix of skeletal hardparts (versus the oft-cited influence of size, gross morphology, and mineralogy), and (2) reproductive fecundity of the shell producer (= rate of total carbonate production).

Durability. Brachiopods have the apparent advantages of calcitic hardparts, relatively large body size, gregarious settlement, mutually attaching behavior and, in many, resistance to disarticulation. In contrast to aragonitic bivalves, however, for which we observe a range of states of preservation, Paleozoic and Mesozoic brachiopods alike

tend to be either well-preserved (intact or fragments) or absent; few exhibit evidence of abrasion, corrosion, and intensive bioerosion (but for exceptions, see Holland in press).

This record could indicate extreme post-mortem durability of brachiopod shells. By their failure to develop significant bioclastic deposits, however, the opposite condition would seem even more likely: that brachiopods undergo very rapid disintegration and have low tolerance to reworking and to post-mortem exposure on the seafloor, lower even than many aragonitic shells. Collins (1985) and others (M. LaBarbera, C. Thayer, P.D. Taylor, pers. comms.) have observed softening of dead shells within several months of post-mortem exposure to seawater and have observed that the ventral margin can disappear from partially buried articulated specimens. Although it has been suggested that punctae may inhibit shell borers during life (e.g., Rudwick 1970:47), these organically lined perforations might also accelerate skeletal disintegration after death (C. Thayer, pers. comm.). Exceptional shell-gravel-forming brachiopods from the early Paleozoic are in fact predominantly impunctate groups (orthides, atrypides, pentamerides, some spiriferides), whereas "modern" terebratulides are almost exclusively punctate.

Thus the preservational Achilles heel of brachiopods may well be the high organic content of the shells (not limited to punctae), in contrast to aragonitic bivalve shells of comparable size which persist despite their seemingly vulnerable mineralogy. The specific failure of Jurassic brachiopods to form major skeletal accumulations would of course have been exacerbated by their much lower abundance and smaller size than earlier Paleozoic brachiopods, a consequence of the Permo-Triassic bottleneck. Recent brachiopods available for actualistic experiments are also small in body size. The organic-content factor is nonetheless tantalizing because it could also explain the rarity of concentrations dominated by bivalves with organic-rich shells, such as mytilids and nuculoids. Both occur in high densities when live and in small groups of articulated, life-position individuals in the fossil record. Bioclastic accumulations in the record are insignificant however even in the case of Cretaceous nuculoids, which attain body lengths of 4 and 5 cm and shell thicknesses up to 1 cm.

Fecundity.-- Some of the most impressive modern, non-reefal bioclastic accumulations are produced by oysters. Rates of egg production among Recent oysters are several orders of magnitude higher than any other living benthos (e.g. 5-115 million eggs per female; Buroker 1985). Modern oyster "reefs" also have the highest rates of benthic carbonate production, again by several orders of magnitude based on standing crop measurements (~7000 to 95,000 g CaCO₃/m²-yr, versus ~2,000 to 10,000 for coral reefs and <500 for level-bottom shelled benthos; E.N. Powell, 1988 pers. comm.). Infaunal molluscs have lower carbonate production and fecundities than oysters (100's of thousands to millions per year for planktotrophic taxa, fewer for non-planktotrophic taxa), but are often still higher than modern brachiopods (100 to 21,500 eggs/yr maximum; data compiled in Valentine & Jablonski 1983). Law and Thayer (1988) has postulated that Paleozoic brachiopods also had modest fecundities comparable to Recent species.

It could be argued that if reproductive fecundity, translated into total carbonate (=bioclast) production, is sufficiently high, then the aggressiveness of the post-mortem environment is secondary -- the effects of processes and agents antagonistic to shell preservation will be overcome. And, as discussed elsewhere (Kidwell 1986, 1989), once shell material accumulates in abundance, the likelihood of its preservation is increased through several kinds of biological, physical, and biogeochemical feedbacks. The oysters represent a particularly advantageous combination of fecundity and skeletal durability.

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Nanogyra, Liostrea, Lopha, Praexogyra) and other taxa (e.g. the bivalve Lithiotis; Naus and Smith 1988) have not yet been plotted. One problem is ambiguity regarding life habit: many oyster accumulations, particularly in the older literature, are described imprecisely as reefs or bioherms. These require field checking to determine whether they are indeed biogenic buildups of mutually attached benthos or, instead, post-mortem bioclastic accumulations or hybrids of these two end-members. Another stumbling block to analysis of these data is the perennial problem of operationally defining or distinguishing between reefs, thickets, and bioclastic concentrations. The gradation between the two readily distinguished end-members is continuous for oysters as for other benthic groups (e.g., Cuffey's 1985 discussion of bryozoan "reef" terminology). A further difficulty with Jurassic oyster data is taxonomic ambiguity: for example, Praexogyra hebridica previously had been assigned to Ostrea (also of family Ostreidae) and to Liostrea (of family Gryphaeidae) (Hudson & Palmer 1976). If the formation of shell concentrations is in some part a phylogenetic attribute, then taxonomic assignments for the dataset must be robust at least to the family level.

Other Groups. Many additional benthic groups can dominate thick bioclastic concentrations in post-Jurassic strata, and these deserve investigation in Jurassic and older rocks. For example in Tertiary sands of the US Atlantic Coastal Plain, loosely to densely packed accumulations dominated by turritellid and olivid gastropods range up to several meters in thickness. Nerineid gastropods formed apparently comparable concentrations up to 1 m at least in thickness in the Jurassic of Europe and North America. With notable exceptions, such as the complexly interstratified Ordovician Loxoplocus gastropod buildup of Kentucky, which thickens locally to 3m (Marble Hill bed, Swadley 1980), the pre-Jurassic record of gastropods appears to be typically archaic in nature.

Bryozoans are another group worth further investigation, inasmuch as cyclostomes and cheilostomes form extensive shell gravels in the Recent and Neogene (e.g., eastern shelf of New Zealand and south Australian shelf, Wass et al. 1970, Nelson et al. 1988; Pliocene Coralline Crag, Balson 1983). Pre-Jurassic cyclostomes apparently did not form shell gravels comparable in scale and dense-packing to Recent examples (Paul Taylor, pers. comm. 1988). Other Paleozoic bryozoans, such as the trepostomes, fenestellids, and fistuloporoids, are more commonly cited for their reef-forming ability than for their bioclastic accumulations but this may be a monograph effect. According to Cuffey (pers. comm., 1988), many Paleozoic examples are known from North America but full descriptions have not been published (e.g., thick trepostome coquinas from the type Cincinnati, Martinsburg Fm, Rodman Ls, Maquoketa Fm, Trenton Ls, Constellaria Ls (all Ordovician), Helderburg Group (Devonian), and west Texas Glass Mountains (Permian); 1-3m thick fenestellid coquinas from Salem Ls and Warsaw Fm (Mississippian)).

Quality of the data. Inspection of the graphs in Figure 1 shows that, in the Jurassic, bivalve-dominated shell concentrations exhibit significantly greater variation in thickness than brachiopod concentrations. Both densely and loosely packed concentrations of bivalves commonly range up to 1 m in thickness and can reach 2 and 3 meters, whereas brachiopod concentrations commonly are only loosely packed at best and range in thickness to only 30 cm.

It is difficult to imagine how these differences could be an artefact of sampling. Most reports -- whether of brachiopod- or bivalve-dominated deposits -- will be biased toward the thickest and densest concentrations as these are visually impressive and often distinctive lithologies. Judging from my experience in the Cenozoic, these deposits are more likely to be commented upon in published reports than small-scale

Any group with high fecundity or carbonate production, however, could overcome vulnerable shell characteristics or aggressive taphonomic environments to accumulate significant bodies of bioclastic material.

CONCLUSIONS

The details of when and how shell gravels have developed in the history of life are unclear, but an initial examination suggests that skeletal accumulations have increased in physical scale and changed in ecological composition over the Phanerozoic. This evolution appears to trace the evolution of shell producers rather than shell destroyers and dispersers, and thus the pattern will in all likelihood be more complex than the initial two-mode hypothesis put forth here. These observations have implications for several lines of geological and paleobiological analysis of the fossil record.

1. Earlier work on Cenozoic strata in local basins indicates that, over time scales of millions to a few tens of millions of years, the nature and distribution of shell concentrations are controlled primarily by patterns of physical sedimentation: skeletal material is strongly associated with stratigraphic hiatuses, and taphonomic features can be used to reconstruct sedimentary dynamics and gradients in the physical environment (Kidwell 1982, 1986, 1988b and references therein). The scale and composition of these concentrations vary among shallow marine environments because of variation in benthic communities, among other factors. The paleontologic nature of hiatal shell accumulations has thus probably changed over longer time scales in the Phanerozoic owing to evolutionary ecology. For example, if Paleozoic faunas do have generally lower fecundities and post-mortem durabilities, then hiatal concentrations will not only have different taxonomic compositions than post-Paleozoic examples, but will also be thinner, less likely to develop, and less likely to show as much taphonomic variation between long and short hiatuses. Descriptions by Parsons et al. (1988) of hiatal concentrations in the Devonian Hamilton Group that are comparable in duration to those of my Cenozoic studies are consistent with these predictions.

2. Any significant change in patterns of skeletal accumulation -- whether related to such factors as the rise and fall of specific shell producers, the evolution of shell destroyers, transgressive-regressive cycles, or the simple elapse of time -- opens the possibility of significant, non-random changes in the documentary quality of the fossil record. These changes might be for better or for worse. For example, if Paleozoic shell gravels on average are composed of less durable hardparts than post-Paleozoic shell gravels, then shorter periods of time-averaging would be indicated. Paleozoic assemblages would be more likely to yield reliable alpha-level measures of diversity (*sensu* Sepkoski 1988) than would post-Paleozoic assemblages, where assemblage diversity values are more likely to reflect both alpha and beta sources. By such a scenario, perceived long-term increases in alpha-diversity could be in part artefactual.

Regardless of the specific implications for bias in the record, long-term biostratigraphic changes are at the very least symptomatic of a more complicated record -- biologically and taphonomically -- than paleontologists would prefer. Species assemblages that have complex post-mortem histories commonly have suffered greater taphonomic "overprinting" (i.e., modification by selective preservation and the admixture of exotic and non-contemporaneous hardparts). The longer time-averaging that typically accompanies such histories also exposes the assemblage to taphonomic feedback, changing the composition of further shell input.

3. Finally, shell gravels represent distinctive benthic habitats and settings for biotic

interactions, both among living organisms and between living organisms and dead shells. The operation of such live:dead interactions (taphonomic feedback), and their probable evolution over the Phanerozoic (Kidwell & Jablonski 1983), make long-term changes in shell gravels all the more interesting: these must be viewed as products of biotic as well as biostratinomic processes. On a larger scale, if the three-dimensionality of shell gravels matters ecologically, then the post-Paleozoic multiplication of thick bioclastic accumulations signifies the elaboration of a distinctive niche in benthic ecosystems, a kind of taphonomic feedback on very long, Phanerozoic time scales.

SUMMARY

Preliminary data on Jurassic shell concentrations in Great Britain indicate both archaic and modern styles, and suggest that long-term changes in biostratinomic features are linked to the phylogeny of shell producers rather than to the evolutionary ecology of shell destroyers and dispersers (e.g., bioeroders, duraphagous predators, bioturbators). Jurassic brachiopod beds tend to be thin, localized concentrations of loosely packed whole specimens; in general, these pavements, nests and "jacks" are taphonomically and paleoecologically fairly simple. It appears that Jurassic articulate brachiopods rarely formed significant bioclastic deposits, notwithstanding their calcitic mineralogy and often gregarious mode of life. Bivalve concentrations on the other hand, whether dominated by epifaunal, infaunal, or semi-infaunal species, include not only small-scale concentrations but also large-scale (>> 0.2m thick), densely packed bioclastic accumulations; many of these have taphonomically and paleoecologically complex histories of reworking and recolonization. Like their younger representatives, Jurassic infaunal bivalves apparently could form thick, dense accumulations despite largely aragonitic shells, and some oysters then as later could also accumulate significant bioclastic deposits despite small body sizes. In general, shell mineralogy, body size, and life habit of shell producers appear to be poor predictors of shell accumulations; skeletal microarchitecture (particularly organic content) and reproductive fecundity may be stronger controls.

ACKNOWLEDGMENTS

I am grateful to D.W.J. Bosence, W.S. McKerrow, and P. Wignall for generous advice in the field and to A. Hallam and D. Jablonski for helpful reviews. Thanks also to them and to many others for valuable comments and encouragement: (in chronologic order) M.J. Simms, A.B. Smith, N.J. Morris, R.J. Cleavelly, A.L.A. Johnson, P.D. Taylor, and T. Aigner on the far shore and, on the near shore of the Atlantic, M.E. Johnson, R.E. Terry, A.I. Miller, D. Springer, C. Bolton, T. deFreitas, T. Sami, C.W. Thayer, C.E. Brett, G.C. Baird, D.B. Blake, J.J. Sepkoski, and R.J. Cuffey. This work has been supported by Shell Foundation, Arco Oil & Gas Company, Amoco Production Company and matching funds from NSF EAR85-52411-PYI.

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January 1989 ms