Patterns in bioclastic accumulation through the Phanerozoic: Changes in input or in destruction?

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ABSTRACT

Evolutionary changes in the ecology and diversity of organisms that produce and destroy calcareous skeletons suggest that bioclastic concentrations themselves might have changed in nature through the Phanerozoic. Empirical data from marine siliciclastic records of Ordovician-Silurian, Jurassic, and Neogene ages indicate a significant increase in the thickness of densely packed bioclastic concentrations over geologic time, from a primarily thin-bedded brachiopod-dominated record in the Ordovician-Silurian to a mollusk-dominated record with many more and thicker shell beds in the Neogene. Jurassic shell beds vary in thickness with the Paleozoic or modern affinities of the chief constituents, suggesting, along with other evidence, that the Phanerozoic increase was determined neither by diagenesis nor by a shift in taphonomic conditions on the sea floor but rather by the evolution of bioclast producers, namely, groups with (1) more durable low-organic skeletons, (2) greater ecological success in high-energy habitats, and (3) on the basis of indirect evidence, higher rates of carbonate production. These results suggest that (1) reproductive and metabolic output has increased in benthic communities over time and (2) the scale of time averaging in benthic assemblages has increased owing to greater hard-part durability of modern groups.

INTRODUCTION

Bioclastic concentrations, i.e., bioclast-supported shell and bone beds, are distinctive and in some instances volumetrically significant elements of the sedimentary record. Analysis of such beds can yield important information about the hydrodynamics of depositional environments, siliciclastic accumulation rates, and postmortem bias in fossil assemblages (see review in Kidwell, 1991). Benthic communities have, however, changed substantially during the Phanerozoic, in terms of both the organisms that produce mineralized skeletons and those that destroy them, so that long-term changes in the nature of bioclastic concentrations are to be expected (see Allison and Briggs, 1993, on possible temporal trends in soft-tissue preservation). For example, the relative abundance, physical dimensions, and preservational quality of densely fossiliferous deposits might have decreased through the Phanerozoic because of increases in aragonitic taxa, bioeroders, shell-crushing predators, and the intensity and depth of bioturbation. On the other hand, these changes might have been counterbalanced or exceeded by the positive effects of larger-bodied benthos and increased diversity of shelled infauna, especially in shallow-water environments. Finally, changes in the bioclastic record might reflect entirely nonbiogenic factors such as diagenesis and paleogeography (e.g., sparsity of epicontinental seas in the Cenozoic). Given the spectrum of possible patterns, we surveyed shell beds in Ordovician-Silurian and Neogene shallow-marine records as end-member periods for the Paleozoic and Modern Faunas of Sepkoski (1981), and we compared these with the Jurassic data set of Kidwell (1990). Even this broad-brush approach detects significant differences in densely fossiliferous deposits through the Phanerozoic.

METHODS

To obtain operational consistency, our analysis was restricted to the thickness and taxonomic composition of bioclast-supported shell beds, and bioclasts ("shells") were defined as carbonate skeletal elements or fragments of >2 mm diameter. To control for variation in shell beds related to physical environmental factors such as seafloor reworking, paleoclimate, and rock accumulation rate, fossiliferous records were surveyed for a comparable range of shallow-marine environments (back-barrier marginal marine to outer shelf), paleolatitudes, and tectonic settings during each study interval (37 Neogene, 44 Jurassic, and 34 Ordovician-Silurian stratigraphic units, primarily in North America and Europe but including Australia and Central and South America). To avoid comparing records with radically different diagenetic histories and to minimize the complications of reefs and boundstones, data collection focused on siliciclastic records; shell beds from biohermal, oolitic, and micritic limestone successions were excluded. In this particular analysis, we also exclude encrinites (crinoid ossicle–supported beds) because so many proved to be either (1) calcarenitic (i.e., bed-supporting ossicles were <2 mm in diameter and thus finer than our minimum for other bioclasts) or (2) so obscured by syntaxial cement that their bioclastic fabrics were difficult to categorize without petrography.

Published reports were used to identify fossiliferous records, but most data are from original field observations (76% of 85 Ordovician-Silurian and 72% of 218 Neogene data points). Within each facies or formation surveyed, each bioclastic accumulation that met the strict operational definition of a shell bed (i.e., a sedimentary deposit supported throughout by bioclasts that are >2 mm in diameter) was tallied. Frequency dis-

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tributions of shell-bed thicknesses were then compared by using the nonparametric Kolmogorov-Smirnov test (Sokal and Rohlf, 1981). The only exception to this system of data tabulation was for shell beds <10 cm thick. For these, we tabulated the number of different *kinds* of shell beds <10 cm thick in a given lithostratigraphic unit rather than tallying every example of each kind. This approach was necessary so as not to be overwhelmed by the virtually uncountable and identical very thin shell beds (e.g., storm beds, turbidites) that characterize some units, as well as to minimize artifactual variation related to the number of outcrops that were available per stratigraphic unit; thicker shell beds can usually be identified uniquely and traced confidently between outcrops, whereas very thin ones generally cannot and thus might erroneously be counted more than once. This procedure produces frequency distributions with a highly conservative minimum value for the first size class. Statistical comparisons were performed by using both the full frequency distribution and one in which the first size category was omitted (p values denoted as full or truncated, respectively).

OBSERVED PATTERNS IN SHELL-BED THICKNESSES

Neogene

Neogene shell beds exhibit a broad range in thickness and taxonomic composition. Thin, decimetre-scale concentrations recording brief events such as storms, opportunistic settlement, and predation are dominant (i.e., define the mode), but shell beds ≥ 50 cm thick are very common (Fig. 1). Aside from submarine debris flows, these thicker examples are internally stratified or thoroughly amalgamated accumulations built by multiple short-term events of reworking and recolonization; they include bioclastic tidal ridges, washover fans, and condensed transgressive facies (e.g., Kidwell, 1991). The frequency distribution does not vary significantly with tectonic setting (full $p > 0.30$, truncated $p > 0.50$) or for field vs. literature sources of data (full $p > 0.50$, truncated $p > 0.20$); however, midlatitude records, which dominate the Neogene data set, might contain significantly more thin shell beds than do low-latitude records (full $p < 0.10$, but truncated $p < 0.005$) (Fig. 2[1]).

Benthic bivalves are the most common dominant bioclast in Neogene shell beds across the full range of thicknesses. Compositions vary from entirely epifaunal and calcitic (pycnodont and ostreid oysters, pectinids, anomiids) to dominantly infaunal and aragonitic (especially mono- and polytaxic bivalve assemblages of arcids, glycymerids, isognomids, chamids, astartids, crassatellids, mactrids, venerids, and corbulids). No single group or life habit is responsible for the tail
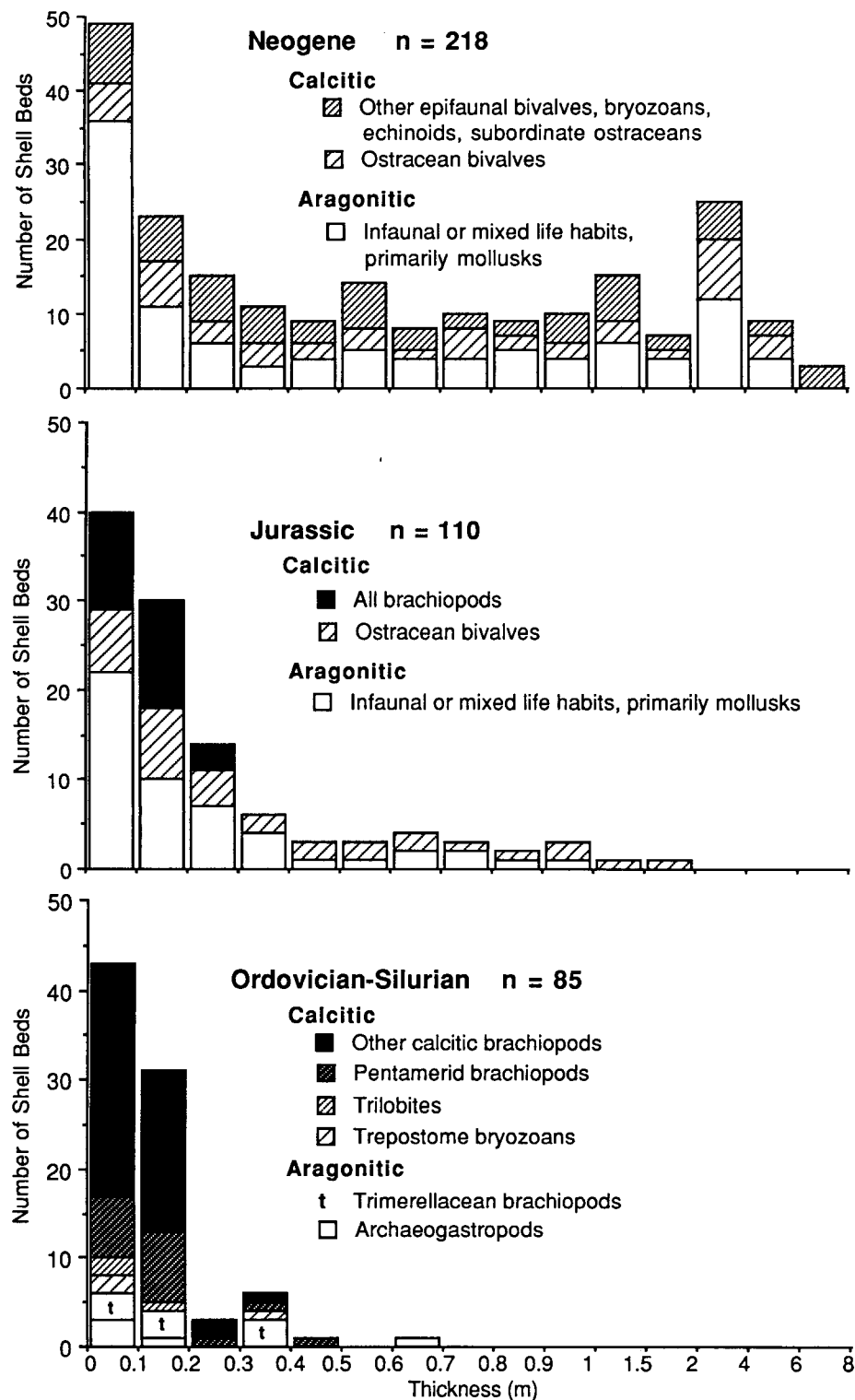

Figure 1. Frequency distributions of thickness of bioclast-supported shell beds (bioclasts > 2 mm, excluding crinoids), showing significant shift to right-skewed distributions over time. Where thicknesses fell at boundary, shell beds were tallied in larger size class. Contrast between Ordovician-Silurian and Neogene data sets reflects evolution of several bioclast-producing groups and does not depend upon single biomineral or life habit.
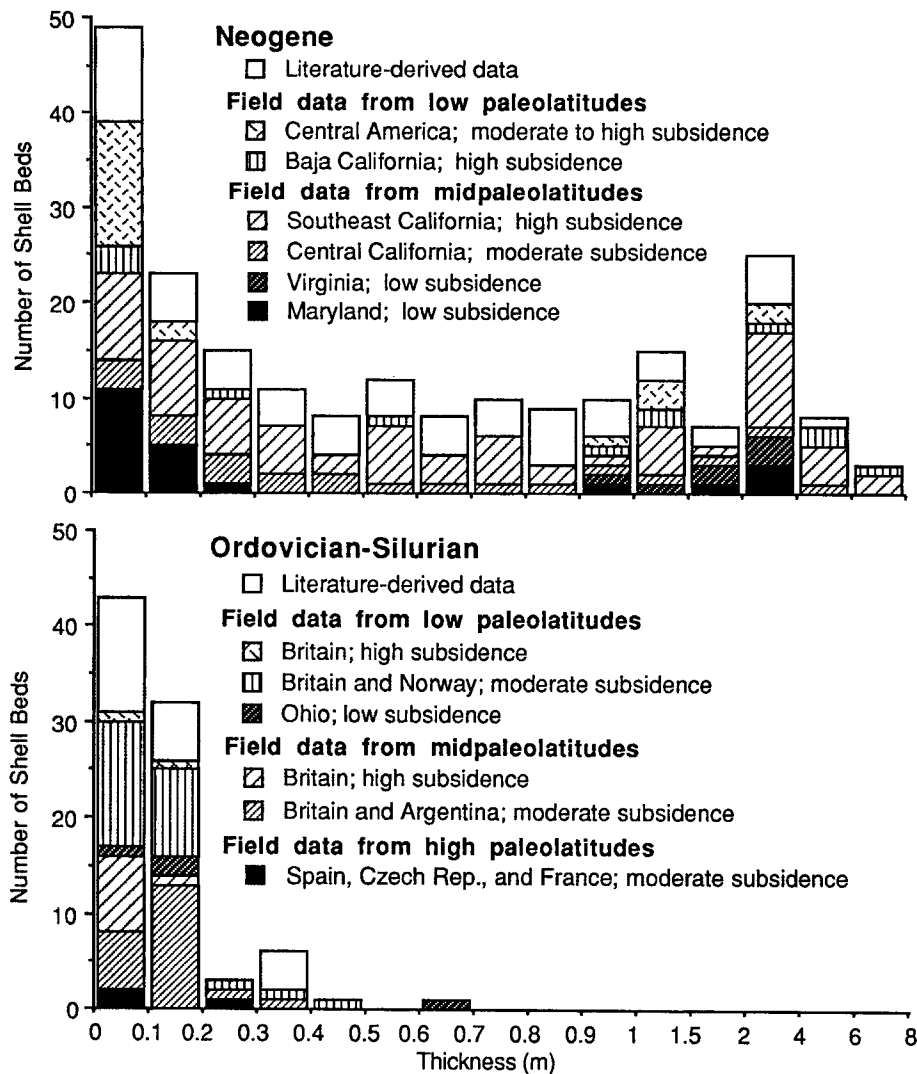
Figure 2. Breakdown of data showing that frequency distributions do not vary significantly with paleolatitude, tectonic setting, or field vs. literature source of data (see footnote 1).

of the frequency distribution (Fig. 1). Cheilostome bryozoans, balanomorph barnacles, irregular echinoids (all calcitic), and various aragonitic gastropods are common subsidiary elements in polytaxic concentrations, and some form monotypic concentrations several metres thick.

Ordovician-Silurian

In contrast, Ordovician-Silurian shell beds (n = 85) are restricted in thickness (87% are <20 cm; 65 cm is the maximum; Fig. 1). Again, most of these thin beds are products of brief high-energy events, particularly storms (e.g., Brenchley and Newall, 1982; Kreisa and Bambach, 1982). Amalgamated multiple-event accumulations (e.g., shell shoals) and more gradually accumulated concentrations (e.g., recolonized shell pavements) are relatively rare and tend also to be thin. The frequency distribution does not vary significantly with paleolatitude, tec-

tonic setting, or data source ($p > 0.20$ for all comparisons) (Fig. 2).

This data set is dominated by calcitic brachiopods, particularly orthids, strophomenids, pentamerids, and atrypids, the shell beds of which are all <50 cm thick. Pentamerids and aragonitic trimerellids also contribute to 1–5-m-thick multilayer buildups formed by repeated opportunistic colonization of quiet sea floors (Johnson, 1977; Webby and Percival, 1983), but these accumulations are not homogeneously densely packed. Instead, relatively thin, densely packed shell beds are separated by equivalent or thicker matrix-supported beds. Trepostome bryozoans also commonly form dense concentrations up to ~40 cm thick and are subordinate contributors to many brachiopod concentrations. Solitary corals, archaeogastropods, and trilobites are generally minor contributors, but we have verified one exceptional 65-cm-thick interval of

densely packed gastropods (outlier in Figs. 1 and 2).

Jurassic

The Jurassic data present an intermediate state. Molluscan concentrations range up to several metres, but brachiopod concentrations closely resemble those of the Ordovician-Silurian (Fig. 1; Jurassic brachiopod distribution is significantly different from that of Jurassic bivalves [both $p < 0.05$], but not from that of Ordovician-Silurian brachiopods [both $p > 0.5$]). Plotted here is the siliciclastic subset of Kidwell's (1990) British data, plus new field data from northern Europe. These data do not have the paleolatitudinal span of the Ordovician-Silurian and Neogene data, but the presence of Tethyan groups (dasycladacean algae, larger benthic foraminifera, and hermatypic corals) in the area for substantial intervals (Aalenian through Bathonian; ecotonal corals only in the Late Jurassic) indicate that tropical as well as nontropical siliciclastic records were sampled. The older 1990 data set was by itself thought to capture the global pattern (A. Hallam, 1988, personal commun., in Kidwell, 1990).

DRIVING MECHANISMS

The data reveal a significant increase in noncrinoidal shell-bed thickness from predominantly thin deposits in the Ordovician-Silurian to a strongly right-skewed record in the Neogene (full $p < 0.01$, truncated $p < 0.05$; Fig. 1). These differences could reflect (1) sampling effects, (2) differences in the extent of diagenesis, (3) evolutionary changes in the community of shell destroyers, or (4) evolutionary changes in bioclast producers.

Sampling

Although these data cannot be comprehensive, the frequency distributions are probably robust approximations of noncrinoidal bioclastic concentrations in these geologic intervals. The number of records available for study favor the Ordovician-Silurian, with five times the duration of the Neogene and twice the outcrop area of the entire marine Tertiary in North America and Europe (Allison and Briggs, 1993). Paleogeographic differences are also an unlikely source of major bias because we sampled comparable arrays of environments (Table 1) and found no strong correlation between shell-bed thickness and either paleolatitude or tectonic setting. We have as yet unverified reports of additional thick shell beds, but the thickest candidates are still ≤1 m thick for the Ordovician-Silurian and ~10 m for the Neogene.

The effect of excluding encrinites is more difficult to evaluate. In the Ordovician-Silurian, crinoid *calcarenites* (i.e., bioclast size mode <2 mm) commonly reach 1–3 m in thickness and exceptionally 10 m in both siliciclastic (S. M. Holland, 1993, personal commun.) and carbonate records (Ausich, 1990). Some of these deposits (or subsidiary layers) might prove to be sufficiently coarse grained to be categorized as shell beds and thus, if included, would shift the Ordovician-Silurian frequency distribution toward that of the Neogene. Crinoids are the only significant potential exception to the otherwise thin-bedded Ordovician-Silurian bioclastic record, however, in contrast to the many taxonomic groups that compose ≥1-m-thick concentrations in the Neogene. Thus, at the very least, a qualitative difference between the Ordovician-Silurian and Neogene records would probably remain.

Diagenesis

If diagenesis culls skeletal carbonate progressively with geologic age, the thinnest shell beds should be removed preferentially. The observed trends, however, could be explained only if diagenesis preferentially removed the *thickest* end of the Ordovician-Silurian spectrum. Furthermore, the presence in the Jurassic of both thick bivalve concentrations and exclusively thin brachiopod concentrations (Fig. 1) suggests that shell-bed thickness depends more on the attributes of particular bioclast producers than on geologic age.

The Ordovician-Silurian vs. Neogene contrast might also arise from selective destruction of aragonite in older rocks, especially since some of the thickest shell beds in our Ordovician-Silurian data set are composed of aragonitic taxa (and see Bambach, 1993). However, even if all aragonite-dominated and mixed calcite-aragonite concentrations were removed from the Neogene data set, simulating severe diagenetic culling, the Neogene frequency distribution still would not resemble the Ordovician-Silurian distribution because 55% of Neogene shell beds ≥1 m thick are composed entirely of calcitic taxa (calcitic Neogene differs from Ordovician-Silurian at $p < 0.001$) (Fig. 1).

Biological Destruction and Dispersion

Although the precise timing and magnitude of the changes are still poorly known, bioerosion, duraphagous predation, and bioturbation are all thought to have increased over the Phanerozoic, with a major acceleration through the Mesozoic (Thayer, 1983; Vermeij, 1987; Crimes and Droser, 1992; Vogel, 1993). This increased taphonomic pressure—including increased sediment irrigation and perhaps increased early diagenetic dissolution—should have reduced the survival of bioclasts and thus their likelihood of forming thick concentrations. The temporal pattern documented here, however, with thick shell beds becoming more common late in the Phanerozoic, is opposite to that expected if these factors were first-order controls.

Bioclast Producers

The strong correlation between the thickness and taxonomic composition of dense shell beds (Fig. 1) suggests that the major control on patterns of bioclastic accumulation has been the evolutionary history of bioclast-producing groups. This is borne out by the Jurassic record, where both brachiopods and bivalves were abundant but formed concentrations of significantly different scale. The Jurassic remnants of the Paleozoic Fauna (brachiopods) continued to produce exclusively thin accumulations, whereas the diversifying bivalves and other members of the Modern Fauna (sensu Sepkoski, 1981) were already generating accumulations similar in scale to those seen in the Neogene. Crinoids continued to be the bioclastic exception among the Paleozoic Fauna, even to the Jurassic (Ausich, 1990). By the Neogene, both the abundance and maximum range of thick shell beds increased (difference from Jurassic is significant at $p < 0.001$), as did the number of groups contributing to such deposits.

Members of the Modern Fauna that form thick bioclastic concentrations all show evidence of (1) highly durable hard parts, (2) ecological success in relatively high energy habitats, and/or (3) high rates of carbonate production. Crinoids shared at least some of these favorable attributes, but other members of the Paleozoic Fauna apparently did not; we believe that this difference explains most of the contrasts in bioclastic facies documented here.

1. Postmortem durability. Many thick concentrations show evidence of complex histories of accumulation involving repeated reworking and time averaging of bioclasts (e.g., mixtures of ecologically, taphonomically, or diagenetically disparate shells, high degrees of shell reorientation and disarticulation, and complex internal stratigraphies including multiple discontinuity surfaces subdividing the shell bed; see Kidwell, 1991), implying that constituent hard parts could survive such treatment. Mineralogy, body size, gross morphology, and life habit apparently are not the determining factors: dominant taxa can be aragonitic or calcitic, small or large, fragile or robust, and epifaunal or infaunal. However, biomineral micro- structure does appear to matter. Thick shell beds are rarely dominated by taxa whose hard parts are built of high-organic microstructures; these include the prismatic calcite found in brachiopods and mytiloid bivalves and the nacreous and prismatic aragonite widespread among other bivalves of the Paleozoic Fauna (exceptions include thick Jurassic and Neogene shell beds of nacreous isognomonid bivalves). In contrast, low-organic microstructures are prevalent among the modern bivalve and other clades that do form thick shell beds (see Collins, 1986, and Glover and Kidwell, 1993, for supporting experimental evidence).

The relatively low durability of most Ordovician-Silurian brachiopods and bivalves is also suggested by two lines of negative evidence (work in progress): (1) the rarity of bored shells notwithstanding bored hardgrounds, suggesting rapid disintegration of microstructures into crystallites, and (2) their failure to form taphonomically complex concentrations on transgressive and other hiatal flooding surfaces, in contrast to those formed by Ordovician-Silurian crinoids (Holland, 1993) and post-Paleozoic mollusks (Kidwell, 1993).

2. Environmental distribution. Habitat preference of bioclast producers is almost certainly also important in the formation of thick shell beds, if only because postmortem winnowing and transport are more frequent in some environments than in others. The inability of brachiopods and trepostome bryozoans to colonize mobile shallow-water substrates in the Paleozoic and the low diversity and abundance of bivalves at that time in those environments (Thayer, 1983; Miller, 1988) are probably major reasons why Ordovician-Silurian shell beds are thin or absent in nearshore facies (again, crinoids are the ecologic and bioclastic exception to this pattern). In contrast, various benthic mollusks as well as cheilostome bryozoans and balanomorph barnacles were well established in these environments by the time of the Neogene, and their shallow-water concentrations dominate that data set.

3. Rate of bioclast production. Some thick shell beds reflect repeated colonization of a site, and even small and/or fragile shells can dominate these if produced in sufficiently large numbers. This style of bioclastic concentration, driven by the population dynamics of species, was not common among Ordovician-Silurian concentrations but does distinguish the thickest shell beds in that data set (i.e., ≥30-cm-thick monotypic shell beds of in situ or locally reworked trimerellids, pentamerids, and archaeogastropods). High fecundity and gregariousness might

also have been factors in the formation of thick regional encrinites (Ausich, 1990). This pathway remained important in the post-Paleozoic, but the maximum thickness of the resulting shell beds increased, as did the number of groups involved. These include virtually monospecific, 1–3-m-thick concentrations of ostreid oysters in the Jurassic and low-diversity 5–10-m-thick accumulations of lophid oysters, epifaunal pectinid and infaunal mactrid bivalves, calyptraeid gastropods, cheilostome bryozoans, and balanomorph barnacles in the Neogene (all dominated by disarticulated or fragmental shells). Observations that living bivalves in general and oysters in particular attain much higher fecundities and growth rates than do living brachiopods (Valentine and Jablonski, 1983; James et al., 1992) are consistent with the taphonomic evidence for higher carbonate production rates among Modern Fauna. Larger body size may also have been a factor. Whereas most Ordovician-Silurian brachiopods rarely exceeded 4 cm in maximum dimension and exceptionally reached 10 cm, Jurassic and Neogene bivalves commonly had adult body sizes of ≥5 cm and robust shells. Bambach (1993) has argued on other grounds for a similar increase in fecundity and perhaps biomass in shelly macrofauna over the Phanerozoic and has suggested that this derives from a general increase in marine productivity.

IMPLICATIONS

These data indicate an overall increase through the Phanerozoic in the thickness of bioclastic concentrations, in the number of ways that thick (≥30 cm) concentrations form, and in the number of taxa that form them. This pattern appears to be a biological signal rather than an artifact of sampling or diagenesis, driven by the evolution and environmental deployment of Modern bioclast-producing groups, which have more durable hard parts and perhaps higher fecundities. The net effect of these factors on bioclast production exceeded the destructive effects of increased biodestruction and bioturbation. This contrasts with the Phanerozoic *decrease* in the frequency of excellent soft-tissue preservation that has been attributed to biological evolution of the postmortem environment and specifically to increasing bioturbation (Allison and Briggs, 1993).

The observed changes in bioclastic concentrations and our particular explanation have a series of geologic and paleobiologic implications. Sedimentologically, for example, the change in thickness is accompanied not only by increased variance in the dynamics of accumulation and perhaps increased

abundance of bioclastic sediments in shallow water, but also by shifts (1) from predominantly calcitic assemblages to calcitic, aragonitic, and mineralogically mixed assemblages and (2) from rolling-stone (crinoidal) to more interlocking bioclastic fabrics in the thickest accumulations. This implies a long-term nonrandom change in the diagenetic reactivity and physical stability of bioclastic facies. Taphonomically, the lower durabilities inferred for most Paleozoic groups imply lesser degrees of time averaging in Paleozoic relative to Cenozoic fossil assemblages and specifically a narrower range of skeletal concentrations associated with discontinuity surfaces. Finally, the diversification of the Modern Fauna in shallow-water habitats might have been characterized by a shift in population dynamics toward higher fecundities and/or growth rates in addition to changes in skeletal durability, body size, and life habit (increased infaunalization). These changes, driven at least in part by Mesozoic escalation in predation (Vermeij, 1987) and combined with the decline in Paleozoic Fauna driven by increasing bioturbation (Thayer, 1983) and the Permian-Triassic extinction, appear to have transformed both the taphonomic and sedimentary nature of the bioclastic fossil record.

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Printed in U.S.A.