Models for Fossil Concentrations: Paleobiologic Implications

Susan M. Kidwell

Paleobiology, Vol. 12, No. 1. (Winter, 1986), pp. 6-24.

Stable URL:

http://links.jstor.org/sici?sici=0094-8373%28198624%2912%3A1%3C6%3AMFFCPI%3E2.0.CO%3B2-D

Paleobiology is currently published by Paleontological Society.

Models for fossil concentrations: paleobiologic implications

Susan M. Kidwell

Abstract.—Four basic types of skeletal concentrations are modeled in terms of changes in sedimentation rate alone. The model categorizes fossil concentrations on the relatively objective basis of their bed contacts, and uses this criterion to infer directional shifts in net sedimentation. This radical simplification of accumulation histories, in which hardpart input is held constant, yields a surprisingly powerful model capable of predicting a broad spectrum of taphonomic and paleobiologic phenomena. *Type I* concentrations grade from less fossiliferous sediments and terminate in omission surfaces; if hardpart supply is held constant, they record a slowdown from positive to zero net sedimentation. *Type II* concentrations are the same as Type I but terminate in erosion surfaces (slowdown to negative net sedimentation), and *Type III* and *IV* concentrations are characterized by basal erosion or omission surfaces, respectively, grade upward into less fossiliferous sediments, and record increases in net sedimentation from negative or zero rates to positive rates. According to the model, samples collected from successive horizons within any of these shell beds will differ in the degree and type of post-mortem bias owing to differing histories of hardpart exposure at the depositional interface. Moreover, because rates of sediment accumulation govern the abundance of hardparts at the depositional interface and thus many of the physical characteristics of the benthic habitat, the dynamics of fossil accumulation have direct consequences for the structure of benthic communities (taphonomic feedback) and for ecologically controlled species morphometry.

The model is highly robust to fluctuations in hardpart input, as judged by its ability to correctly infer modes of formation of concentrations in synthetic stratigraphic sections. In addition, field examples of Type I–IV concentrations show independent evidence of formation during intervals of reduced net sedimentation, and many exhibit trends in taphonomic and paleobiologic features expected from the postulated changes in net sedimentation. The model thus provides a testable working hypothesis for the accumulation of fossil material in a wide range of environments, and should be applicable to concentrations of any taxonomic composition, state of preservation, or geologic age. The power and robustness of this heuristic model in fact argue that fossil-rich and fossil-poor strata provide fundamentally different records of past conditions, and that sedimentation rather than hardpart input is the primary control on the nature of the fossil record.

Susan M. Kidwell. Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637

Introduction

One of the most obvious features of the stratigraphic record is the uneven distribution of fossil material. Rather than being uniformly distributed through sedimentary sequences, fossils are concentrated on all scales from small fecal pods and bedding plane pavements to basinwide deposits produced by shelly shoals. Because paleontologists naturally tend to focus on these richest parts of the record, it is important to understand how processes of hardput concentration can alter paleontologic data and the significance of comparing data from different sources.

Studies of post-mortem processes in modern environments and in the fossil record have stressed the diagnostic behavior of hardparts under a range of hydrologic, biologic, and chemical conditions (for reviews, see Schäfer 1972; Müller 1976, 1979; Behrensmeyer and Hill 1980), and this work provides an operational framework for assessing bias in fossil assemblages. Largely lacking, however, has been an evaluation of the consequences of the concentration process itself. Despite investigations into the origin of shell and bone beds in many environments, there is not yet a general model which explains the distribution and nature of concentrations across a spectrum of environments, or which guides the comparison of assemblages from different kinds of concentrations.

The model presented here explores the taphonomic and paleobiologic significance of fossil abundance, approaching the problem for level-bottom settings in terms of the basic factors of rates of accumulation of hardparts versus nonbioclastic sediment. It predicts that fossil-rich and

fossil-poor strata are qualitatively different, both as records and as settings for paleobiologic processes, and leads to a more general hypothesis that variation in the dynamics of sedimentation rather than hardpart input serves as the primary control of the nature of the fossil record.

Basic Rate Relations

On the most basic level, the abundance of fossil material is a function of the relative rates of hardpart input and sedimentation at the accumulation site (Johnson 1960). Relatively enriched fossil deposits arise (1) when hardpart input increases against a background of constant sedimentation, (2) when rate of sedimentation decreases against a background of constant hardpart input, or (3) when both rates vary such that hardpart input increases relative to sedimentation. A fossiliferous deposit embedded within a less fossiliferous sequence can thus be regarded as the outcome of some favorable balance or dynamic shift in these two rates.

Although conceptually straightforward, the hardpart input–sedimentation relationship is complicated because both rates are net rates. Net rate of hardpart input (R-hardparts), for example, is the volume of hardparts supplied per unit time that survive to final burial.[1] It is a function of (1) the rate at which hardparts are supplied to the accumulation site from in situ biological production, transport from allochthonous sources, and reworking of older hardparts, and (2) the rate at which those hardparts are destroyed at

the site (or otherwise removed) before they can be buried permanently. Processes of hardpart destruction include: mechanical abrasion and fragmentation (Chave 1964; Driscoll 1967, 1970; Hollman 1968; Force 1969; Taylor and Layman 1972; Driscoll and Weltin 1973); erosion and transport out of the area (Cadée 1968; Lindberg and Kellogg 1982; Aigner and Reineck 1982; Futterer 1978a, b; Jervey 1974; Johnson 1957; Lever 1958; Lever et al. 1961; Lever and Thijssen 1968); bioerosion, including boring, rasping, and fragmentation (Carter 1974; Futterer 1974; Golubic et al. 1975; Warme 1975); dissolution both at the depositional interface (subaerial weathering, undersaturated seawaters) and during shallow burial (undersaturated porewaters, high or low pH and alkalinity) (Alexandersson 1972, 1978; Anderson et al. 1973; Lewy 1975; Behrensmeyer 1978; Flessa and Brown 1983; Peterson 1976; Aller 1982); and recycling of hardparts through repeated burial-exhumation episodes.

Sedimentation (R-sediment) is similarly a net rate and indicates the fraction of the total volume of sediment deposited per unit time which actually enters the permanent stratigraphic record. For a given rate of hardpart input, low rates of sedimentation favor the formation of fossil concentrations, but the detailed dynamics of the regime of low net sedimentation determine the pattern of fossil accumulation (Fig. 1). For example, regimes of erosion (negative net sedimentation) generate hardpart concentrations through (1) the selective winnowing of fine matrix, which leaves a lag of immovable skeletal elements at the sediment : fluid interface, and (2) the hydraulic reworking of both sedimentary matrix and hardparts with local redeposition of hardparts, such as during cliff or channel margin retreat and very vigorous storm events. Sedimentary omission (zero net sedimentation), on the other hand, concentrates hardparts passively through the failure of sediment to dilute them. Omission results from: (1) the lack of even temporary deposition of sediment supplied to the site (total passing of sediment in suspension; supply is high, total and net sedimentation are zero); (2) the failure of depositional increments to accumulate permanently (dynamic bypassing of sediment in bedload, for example as a mi-

---

[1] Operationally, final burial is defined as burial to sufficient depth within a sedimentary substratum for a hardpart: (1) to attain a refuge from further small-scale episodes of exhumation and exposure at the depositional interface, and (2) to escape destructive early diagenetic porewater regimes. Practically speaking, this means burial to a level that is below the base of hydraulic traction within the sediment and below the zone of bioturbation and strongly fluctuating redox reactions.

The destruction of hardparts continues through later diagenesis, metamorphism, and weathering, but these processes are not considered here because they affect the ultimate preservation of a fossil concentration rather than the dynamics of its formation. In some situations, processes such as differential compaction (e.g., Fürsich and Kauffman 1984) and selective pressure solution of matrix (Wanless 1979; Eller 1981) can further concentrate hardparts after final burial as defined above. This accentuation of primary concentrations is probably of only minor importance compared to processes that operate at the depositional interface.
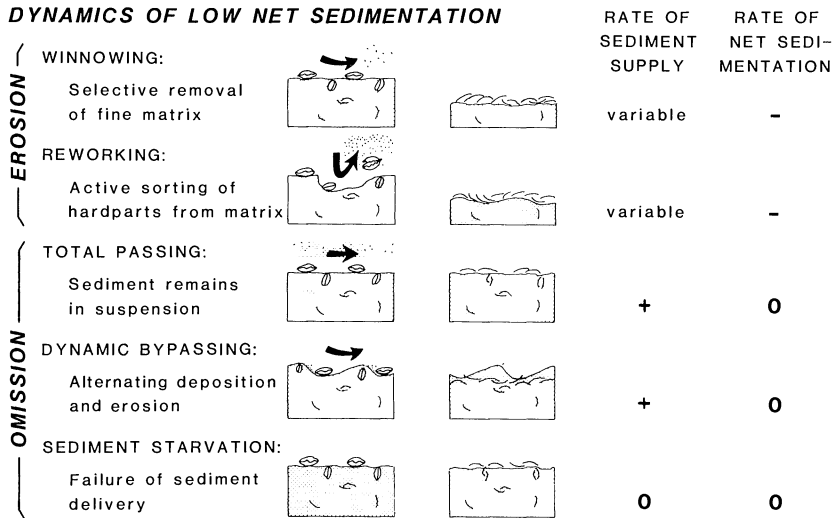
DYNAMICS OF LOW NET SEDIMENTATION

FIGURE 1. The timing and magnitude (dynamics) of sediment supply, deposition, erosion, and transport govern patterns of hardpart accumulation during regimes of low net sedimentation, which are characterized by zero or negative net rates of sediment accumulation. The exhumation-burial histories of hardparts during the concentration process and their close-packing in the final deposit are both functions of the dynamics of low net sedimentation alone: the initial abundance and attitudes of hardparts in the substratum are the same in all five situations. In benthic settings, the dynamics of sedimentation also influence the paleoecologic composition of fossil concentrations through environmental parameters such as water turbidity, frequency of seafloor disturbance, and the formation of firm, shell gravel substrata.

grating ripple train; supply and total sedimentation are high, net sedimentation is zero); or (3) the failure of an appreciable sediment supply to reach the accumulation site (sediment starvation; supply, total, and net sedimentation are all zero). During dynamic bypassing, hardparts accumulate below the sediment: fluid interface at the base of the traction zone.

Patterns of fossil accumulation are further complicated by the fact that net rates of hardpart input and sedimentation vary over both space and time, and can vary in phase and out of phase with each other, dependently and independently. Low net sedimentation itself is a double-edged sword with respect to net hardpart input. On the one hand, all regimes of low R-sediment favor the concentration of fossil material at least hypothetically by reducing the degree to which hardparts are diluted by sediment. At the same time, however, low R-sediment delays the burial of hardparts and increases their likelihood of destruction by processes operating at or near the depositional interface. Some dynamics of low net sedimentation will be marked by higher rates of hardpart destruction than others: for example, erosional reworking and dynamic bypassing are expected to have high rates of abrasion, whereas winnowing and omission might be characterized

by especially high rates of bioerosion. The threshold at which the destructive consequences of retarded burial outweigh the positive effects of low dilution will determine whether an episode of low net sedimentation yields a relative concentration of fossil material.

Selective colonization and mortality patterns of benthos under different sedimentary regimes (e.g., Crisp 1976; Jumars and Nowell 1984; Nowell and Jumars 1984; Probert 1984) and in response to the development of firmgrounds and hardgrounds (Rhoads 1970; Fürsich 1979; Brett and Brookfield 1984) indicate that hardpart input can covary with sedimentation rates for biological reasons. Quantitative rate relationships are extremely difficult to reconstruct from the ecological literature: benthic productivity is usually expressed in terms of biomass rather than volume of hardparts and is related to physical environmental factors such as dissolved oxygen, temperature, salinity, and substratum type rather than to net or total sedimentation rates (e.g., Moore 1972; Driscoll et al. 1974; Hill et al. 1982; Pfannkuche et al. 1983).

Despite the great array of variables that influence rates of hardpart and sediment accumulation, and the complex dynamics of changes in these rates over space and time, only a few net

vectors of combined change in R-hardparts and R-sediment can produce fossil concentrations out of initially fossil-poor substrata, and this suggests a means of summarizing and better understanding the spectrum of possible accumulation histories.

R-Sediment Model

A survey of fossil concentrations in the Miocene Calvert and Choptank formations of Maryland (Kidwell 1982a, 1982b, in prep.) indicated that very few shell beds in these highly fossiliferous shallow marine strata lack evidence of some period of low net sedimentation or hydraulic reworking. The rare, strictly biogenic concentrations (estimated to be well less than 10% of all concentrations) include lenses of broken shells concentrated probably by molluscivorous rays, and monospecific autochthonous clumps of oysters, mussels, turritellid gastropods, and irregular echinoids which record the gregarious life habits of the hardpart producers. In contrast, most of the Miocene fossil concentrations show evidence of either initial accumulation or later modification by a period of omission or erosion. This evidence includes: winnowed sedimentary matrix; reoriented, disarticulated, and overpacked infaunal shells; physical amalgamation of discrete shell horizons into larger-scale, internally complex beds, often preserving pockets of the original, unreworked sediment; admixture of shells in different states of preservation; and bioerosion or encrustation of exhumed infaunal shells.

Identifying an interval of reduced net sedimentation as a common denominator in the formation of shell beds may characterize the Maryland Miocene and probably a majority of shallow marine records, but it fails to explain the variety of taphonomic histories and features possible within the class of sedimentologic shell beds. However, almost all of the sedimentologic shell beds in the Maryland Miocene are associated with stratigraphic discontinuities, either bedding planes or unconformities (tabulated in Kidwell 1982b, in prep.). Concentrations of fossils lie either on top of or immediately underneath sharp discontinuity surfaces recognized by a lithologic change or a physical parting in the rocks; they are "Sohlbanke" and "Dachbanke" (sole beds

and roof beds) in the descriptive sense of Brinkmann (1929).

This association of fossils with bedding surfaces suggests that it is not the interval of low net sedimentation itself but the nature of the change in net sedimentation that determines many of the features of hardpart concentrations. The straightforward and relatively objective field criterion of bed contacts has genetic significance because the upper and lower contacts of a shell bed—whether sharp or gradational—not only indicate the physical relation of the shell bed to surrounding units, but relate the process of hardpart concentration to processes responsible for surrounding less fossiliferous sediments. Where the original nature of bed contacts has not been irrevocably obscured by bioturbation, pressure solution, or other post-depositional processes, sharp contacts indicate disjunct shifts in sedimentation and usually mark an episode of erosion or omission (Barrell 1917; Campbell 1967; Tipper 1983). Hardpart concentrations having sharp primary contacts can thus be interpreted in terms of a change in net sedimentation, either away from or toward the state of zero or negative R-sediment responsible for the discontinuity surface.

On the basis of their stratigraphic contacts, shell beds are categorized into four types (Fig. 2) depending on whether the upper or lower contact is sharp, and whether that sharp contact shows scour and truncation evidence of erosion or merely omission. These four simple kinds of shell beds—abstracted from field examples in the Maryland Miocene—are modeled heuristically in terms of changes in net sedimentation, with the assumption that hardpart input is held constant (Fig. 2). Later in the paper, the model is demonstrated to be robust to deviations from this unrealistic assumption. As an additional simplifying assumption, changes in sedimentation are assumed to be gradual and monotonic.

Ideal shell bed types

Type I shell beds grade from less fossiliferous strata and terminate in nonerosional (omissional) bedding plane surfaces (Fig. 2). Assuming hardpart input is constant, they record a decrease in sedimentation rate from positive (net deposition) to zero (omission) values and should exhibit an upward increase in shell packing density. The

MINIMUM NET SEDIMENTATION RATE

	Zero (Omission)	Negative (Erosion)
Slowdown from + to 0 or −	I	II
Increase from 0 or − to +	III	IV

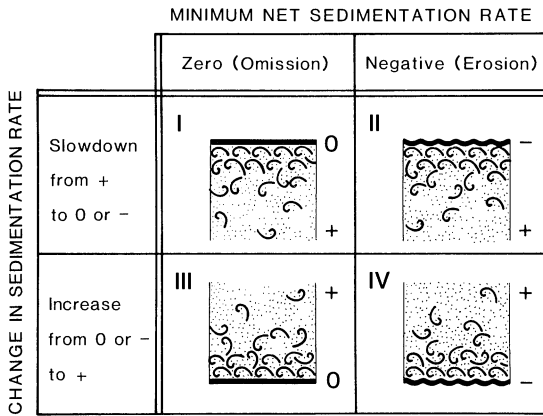(Vertical axis label: CHANGE IN SEDIMENTATION RATE)

FIGURE 2. If hardpart input is assumed to be constant, fossil concentrations having sharp lower or upper contacts must accumulate during a change in net sedimentation. In the situation of Type I and II shell beds, which terminate in omission and erosion surfaces respectively, hardparts accumulate during a slowdown in net sedimentation from the positive rates responsible for shell-poor sediments to the zero or negative net rates required to form the upper discontinuity surface (bedding plane or unconformity). Type III and IV shell beds, which rest on top of discontinuities, form in the context of an increase in net sedimentation.

top of the bed will be a shell pavement that records the final stage of zero net sedimentation (sedimentary omission). Such a decrease in net sedimentation rate can result from: (1) a reduction in sediment supplied to the accumulation site, causing progressive starvation, or (2) the attainment of baselevel equilibrium and a condition of sedimentary bypassing, accomplished either by aggradation of the depositional interface or by a local downward shift in baselevel (e.g., Wheeler 1964).

Type II shell beds grade from less fossiliferous strata and terminate in erosional surfaces (Fig. 2). Under the conditions of the model, they will show an upward increase in shell packing density in response to decreasing sedimentation rates from positive (deposition) through zero (omission) to final negative (erosion) values. Erosion will proceed to rework hardparts from the just-formed shell bed until an erosion-resistant pavement forms along the top. This kind of change from aggradation to erosion proceeds by (1) the local depression of baselevel from a position above the original depositional interface to one below it, (2) the temporary elevation of the depositional interface above local baselevel by uplift or by disequilibrial aggradation, or (3) some combination of these changes.

Type III shell beds are the inverse of Type I shell beds. They rest on sharp, omission surfaces and grade upward with diminishing shell packing density into less fossiliferous sediments (Fig. 2). These beds reflect a shift from initial omission to positive rates of net sedimentation that exceed the rate of hardpart input. The dynamics of such a change can involve: (1) the resumption of sediment supply to a starved site; or (2) where omission was characterized by the bypassing of an appreciable sediment supply, the elevation of local baselevel to lie above the depositional interface rather than coincident with it.

Type IV shell beds are the inverse of Type II shell beds. They rest on sharp, erosion surfaces and grade upward with diminishing shell packing density into less fossiliferous sediments (Fig. 2). These beds reflect an increase in net sedimentation rate from negative (erosion) through zero (omission) to positive (deposition) values. The dynamics of such a change require a relative rise in baselevel from an initial position below the original depositional interface to some position above it, along with a sufficient supply of sediment to aggrade the substratum during the final phase of shell bed formation.

Taphonomic and Paleobiologic Predictions

Post-mortem bias

During the accumulations of ideal Type I and Type II shell beds, hardparts are exposed at the depositional interface for increasingly long periods of time.[2] Consequently, assemblages collected from successively higher horizons within such shell beds should show a greater frequency (number of hardparts affected) and intensity (severity of effects per hardpart) of post-mortem destruction by boring, fragmentation, abrasion, dissolution on the seafloor, and subaerial weathering (Fig. 3). Assemblages collected from the top of Type I and II shell beds should also exhibit the highest frequency and intensity of

---

[2] Rate of hardpart burial is extrapolated solely from rate of nonbioclastic sedimentation: vertical mixing and burial of hardparts by bioturbators are ignored. Although burrowing organisms and especially "conveyor-belt"-type infaunal deposit feeders can overturn sediments at prodigious rates (e.g., Rhoads 1967; Cadée 1979), densely packed shell material should inhibit or reduce their effectiveness significantly. As a first approximation, it thus seems unlikely that bioturbation could reverse or nullify the trend in hardpart residence time expected from modeled changes in sedimentation rate.
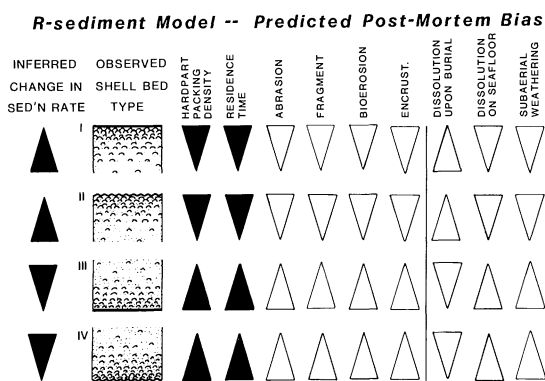
FIGURE 3. Hardpart abrasion, fragmentation, bioerosion, and encrustation are functions of hardpart residence time at the depositional interface, and thus the frequency and intensity of these kinds of post-mortem bias should increase among paleontologic samples collected at successively higher horizons within a Type I or II shell bed. Type III and IV concentrations will exhibit the opposite trends. Expected trends in selective hardpart destruction from dissolution and weathering at or just below the depositional interface are explained in text, as are differences in bias expected among the four shell bed types. Width of triangles increases with increasing bias expected from post-mortem processes.

hardpart infestation by encrusting organisms, and the greatest degree of time averaging of successive living populations owing to slow rates of hardpart burial (Fig. 3).

Despite the negative effects of prolonged residence time on the seafloor, calcareous hardparts that accumulate in abundance are more likely to survive shallow burial than are hardparts dispersed more sparsely through sedimentary matrix, owing to various density-dependent effects during early diagenesis. Abundant hardparts change the texture of the substratum and promote porewater exchange with saturated overlying waters by propping open the sediment, and abundant hardparts evidently can create their own favorable early diagenetic microenvironments once buried (e.g., Sepkoski 1978; McCarthy 1979). In contrast, dispersed calcareous hardparts in pervasively bioturbated sediments have a lower preservation potential due to the lowering of porewater pH by carbonic acid produced through microbial decomposition of organic matter (Aller 1982). Hardpart assemblages in the upper parts of Type I and II shell beds should thus exhibit less evidence of dissolution during burial than those found lower within the shell bed (dissolution upon burial, Fig. 3). These early diagenetic differences between initially

hardpart-rich and hardpart-poor deposits should accentuate primary differences in hardpart abundance arising directly from changes in net sedimentation (or from any other process of hardpart concentration). In contrast, hardpart destruction by leaching in undersaturated overlying waters or by subaerial exposure will be most severe in the upper part of Type I and II shell beds owing to long hardpart residence times at the depositional interface. Similar but inverted trends in these features are predicted for Type III and IV shell beds. During accumulation of these shell beds, hardpart packing density and residence time at the depositional interface gradually decrease (Fig. 3).

Comparison of accumulation histories involving omission (Type I and III) with those including a phase of erosion (Type II and IV) yields further taphonomic predictions. Type II and Type IV shell beds should show more severe time averaging of successive, ecologically or hydraulically distinct assemblages in the most densely fossiliferous part of the concentration than Type I and III shell beds formed over the same length of time, owing to greater vertical mixing of hardparts during erosion than during omission. In addition, the formation of "destructional" Type II and IV shell beds is more likely to (a) involve destruction and removal of less durable and more easily transported hardparts, leaving a residual fossil assemblage sensu Fagerstrom (1964), (b) incorporate allochthonous elements delivered by the relatively high-energy eroding currents or waves, producing a mixed allochthonous-parautochthonous assemblage, and (c) involve the exhumation and admixing of significantly older hardparts with younger remains (biostratigraphic condensation sensu Heim 1924, 1958; Jenkyns 1971).

Finally, Type I and II shell beds will differ from one another in the degree of detail in which the accumulation process is recorded. Whereas the slowdown in net sedimentation will be recorded faithfully within a Type I shell bed, microstratigraphic evidence of this slowdown in a Type II shell bed will tend to be destroyed by the final phase of erosion. The extent to which a Type II shell bed is reworked (or cannibalized) by late-phase erosion, and thus the degree to which the details of the accumulation history are lost, depends on the vigor of erosion and how
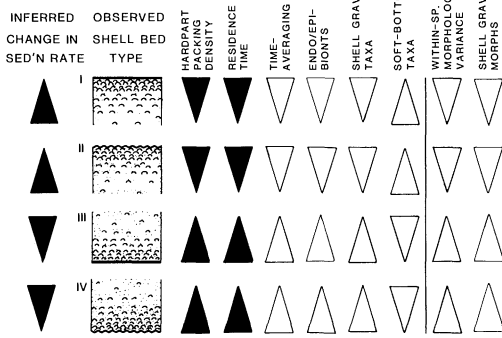
FIGURE 4. The changing residence time of hardparts at the depositional interface, and changing abundance of dead hardparts in the substratum, have biological consequences for the benthic community which should be reflected in the ultimate composition of the fossil deposit. Type I and II shell beds record the transformation of an initially soft-bottom, shell-poor substratum into an increasingly coarse-grained and firm shell gravel habitat. This will favor colonization by fouling organisms and shell gravel taxa while inhibiting the continued success of soft-bottom, primarily infaunal taxa, resulting in an upsection shift within the shell bed toward epifaunal dominance or ecologically mixed assemblages. The observed variance and mean morphometry of ecologically-plastic (ecophenotypic) species can also shift upsection, both because of morphological response of these species to an increasingly shelly substratum, and because of the increasingly time-averaged nature of the assemblage (see Fig. 5). Trends in Type III and IV shell beds will be reversed.

quickly an erosion-proof pavement forms. Hypothetically at least, a Type II shell bed can be transformed into a Type IV shell bed by complete reworking in the erosional phase. This is especially likely where the original concentration is relatively thin.

To summarize between-type taphonomic trends, the overall severity of post-mortem bias from abrasion, fragmentation, size and shape sorting, and time averaging should *increase* from (1) Type I and III concentrations in which omission was characterized by sediment starvation or total passing (least destructive), to (2) Type I and III beds in which omission was marked by dynamic bypassing (alternating deposition and erosion); (3) Type II and IV shell beds in which erosion was accomplished by winnowing; and, finally, (4) Type II and IV shell beds characterized by vigorous reworking (most destructive). The destructive effects of bioerosion should *decrease* along this same array of shell beds because of the inhibiting effects of water turbidity and

physical disturbance on the seafloor during bypassing and erosional regimes.

Benthic ecology

Paleoecologically, the upward increase in shell packing density within Type I and Type II shell beds records the transformation of an initially soft, shell-poor substratum into a shelly and thus coarser and firmer benthic substratum. This progressive increase in hardpart abundance will change the structure of the living benthic community in specific ways, since the presence of dead hardparts in the benthic habitat will facilitate colonization by some adaptive types while inhibiting the success of others by changing seafloor mass properties and the availability of hard substrata for attachment. This concept of live : dead interactions as a driving mechanism for community change has been termed taphonomic feedback (Kidwell and Jablonski 1983).

During the formation of a Type I or II shell bed, hardparts reside on or near the seafloor for longer periods of time and become more abundant, facilitating colonization by species which require hard attachment sites either as larvae, adults, or for egg cases, or which prefer coarse, firm, or topographically complex substrata. These include endo- and epibionts, vagile and sessile free-living epifauna, byssate or otherwise attached epifauna, and small-bodied, primarily shallow-burrowing infauna capable of occupying sedimentary interstices or tolerant of semi-infaunal positions in the seafloor (shell gravel fauna in Fig. 4; see references cited in Kidwell and Jablonski 1983). At the same time, the accumulation of dead hardparts will inhibit the continued success of many deposit feeders in the habitat (especially the larger-bodied skeletized deposit feeders): dead hardparts interfere with organism mobility in the substratum and increase patchiness in sediment grain size, both reducing feeding efficiency. Large-bodied and deeply burrowing suspension-feeding infauna are also expected to be progressively excluded by the restriction and eventual elimination of habitat space (soft-bottom taxa in Fig. 4).

The upper, most densely fossiliferous parts of Type I and II shell beds should thus contain ecologically mixed fossil assemblages recording the successive occupation of the substratum by
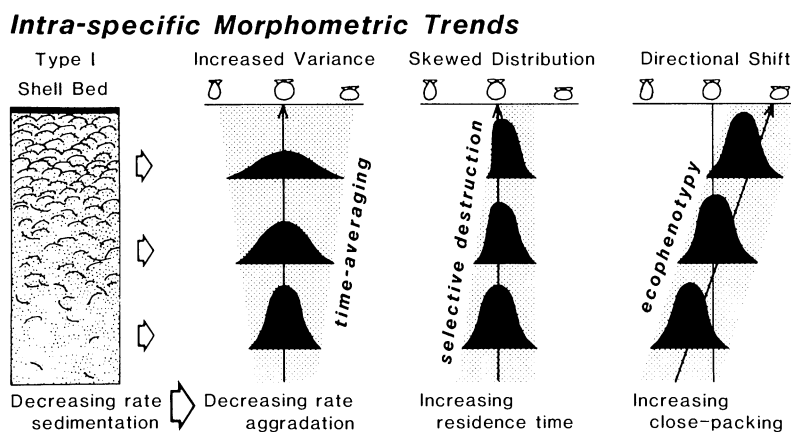
Intra-specific Morphometric Trends

FIGURE 5. Intraspecific morphometric trends observed within Type I shell beds can be consequences of both taphonomic and ecological responses to the slowdown in net sedimentation. A. As a consequence of the slowing rate at which the shell bed aggrades (builds upward), assemblages become increasingly time-averaged; through the mixing of normal background fluctuations in morphology, samples will show increasing morphometric variance upsection. B. With increasing residence times at the depositional interface, assemblages of dead hardparts are more likely to suffer selective destruction, especially of fragile and easily transported morphs, thus skewing the morphometric composition of samples upsection. C. An eco-phenotypic (ecologic) response on the part of a species to increasing abundance of hardparts in the substratum will result in a directional upsection shift in average morphometry toward shell-gravel morphs. Each of these represents an alternative hypothesis to microevolutionary explanations for similar trends.

infaunal- and epifaunal-dominated benthic communities. Sedimentary omission or erosional reworking during the final phase of shell bed formation will contribute to the mixing of successive, ecologically disparate death assemblages, further smearing the record of sequential change driven by taphonomic feedback. Fossil assemblages collected from successive horizons within Type I and II shell beds should thus shift from soft-bottom dominance toward increasingly mixed infaunal-epifaunal compositions or epifaunal dominance (Fig. 4). This pattern should hold whether the initial soft-bottom community drives itself toward local extinction by the in situ accumulation of its own hardparts or wanes because of the introduction of allochthonous hardparts.

In Type III and IV shell beds, taphonomic feedback is responsible for maintaining the shell gravel composition of the benthic assemblage once an initial concentration of hardparts has been established on the discontinuity surface. This initial concentration can result from biological colonization of the discontinuity surface, as in mud-colonizing snow-shoe strophomenids in Ordovician brachiopod-bryozoan pavements (Walker and Alberstadt 1975). Initial hardpart concentrations may also form through in situ

reworking of hardparts or their delivery from allochthonous sources (e.g., Triassic epifauna-colonized storm lags, Aigner 1982). The effects of taphonomic feedback on the composition of fossil assemblages lessens in the later stages of accumulation of Type III and IV shell beds because of accelerating sedimentation, which reduces hardpart abundance and residence time near the seafloor. This trend is in contrast to that within Type I and II shell beds.

Morphometric patterns

In Type III and IV shell beds, the most prolonged time-averaging occurs during the initial phase of shell bed formation, when R-sediment is at a minimum value; in Type I and II shell beds, this trend is reversed. These patterns in time averaging have a number of implications for evolutionary and systematic analysis of morphometric data (Kidwell and Aigner 1985).

The most obvious is that prolonged time averaging, by mixing successive biological populations into a single sampling population, can artificially increase the observed morphometric variance for the species in that horizon. The more prolonged the time averaging, the greater the likelihood of mixing hardparts from extreme random fluctuations or directed trends in species

morphometry into a single assemblage, and thus the higher the probability of inflated variance in the paleontologic sample (see within-species morphometric variance, Figs. 4 and 5). Consequently, sampling through Type III or IV shell beds can artificially generate patterns that mimic evolutionary predictions (Fig. 4), e.g., of speciation as a burst of morphometric variation that dwindles later in the species' history (e.g., Sylvester-Bradley 1977; Williamson 1981, 1982).

Depending on the sedimentary dynamics of the reduced R-sediment interval, selective destruction or removal of morphological outliers might overwhelm the effects of time averaging to reduce variance and skew the morphometric distribution (see selective destruction in Fig. 5). Assemblages in destructional Type II and IV shell beds are more likely to be biased in this way than assemblages from Type I and Type III shell beds owing to enhanced physical destruction of hardparts during erosional reworking and winnowing.

Because many benthic species vary morphometrically (i.e., ecophenotypically) with habitat parameters such as water salinity, water energy or depth, and substratum characteristics, morphometric trends through shell beds can record a genuine biotic response to changes in the benthic environment during the period of hardpart accumulation. Increasing shelliness in the substratum might produce a directional shift in a species' average form (or population variance) away from soft-bottom morphs toward shell gravel morphs as sampled in successive horizons within a shell bed (Kidwell and Aigner 1985; Figs. 4 and 5). Such morphometric trends are more likely to develop in shell beds formed over long periods of time relative to the generation times or longevity of individuals (e.g., accumulation over tens to hundreds of years) than in more rapidly formed shell beds. In shell beds that form over even longer periods of time (e.g., thousands or tens or thousands of years), the shell gravel habitat could conceivably serve as a setting for true, heritable evolution in morphology, although this will be difficult to distinguish from morphometric changes caused by ecophenotypy (Kidwell and Aigner 1985). The nature and extent of morphometric bias in fossil assem-

blages is thus a function not only of the physical and biological dynamics of hardpart accumulation but of the time scale of accumulation as well.

Evaluation of Model

Heuristically, this approach has several advantages. Unlike models based on specific processes such as storm reworking or shoal migration, the abstract R-sediment model can be applied to concentrations of a range of physical dimensions and time intervals of accumulation. For example, the Type IV shell bed describes the features of (and thus provides a testable hypothesis for the origin of) rapidly formed, thin storm lags of shells as well as laterally extensive shelly sands produced during marine transgression: both rest on erosional surfaces (scoured bedding plane and disconformity) and grade upward into less fossiliferous deposits (sediments accumulated as storm energy wanes or during fair weather conditions, and strata recording stillstand or regression). The model can also address concentrations of any taxonomic composition, geologic age, or environment of accumulation, and predicts the distribution of fossil concentrations in the stratigraphic record. For example, Type II concentrations should be rare because of the problem of reworking into Type IV beds; Type II and IV concentrations should dominate higher-energy shoreline and offshore shoal environments, whereas Type I and III beds should dominate distal and low-energy settings; and large-scale/long-term Type III and IV concentrations will characterize the lower boundaries of depositional cycles (base of transgressive-regressive cycles; onlap, downlap, and truncation of depositional sequences), whereas Type I and II concentrations will mark upper cycle boundaries (top of shallowing-up cycles, toplap) (Kidwell 1982a, 1985, in prep.).

The flexibility of the model and the breadth of its predictions nonetheless beg the question of whether the model is true: (1) does the model work under more realistic conditions in which hardput input is allowed to vary? (2) how well does the model explain the origin of fossil concentrations in the stratigraphic record, that is, can it be used in an inverse mode to guide paleontologic analysis?
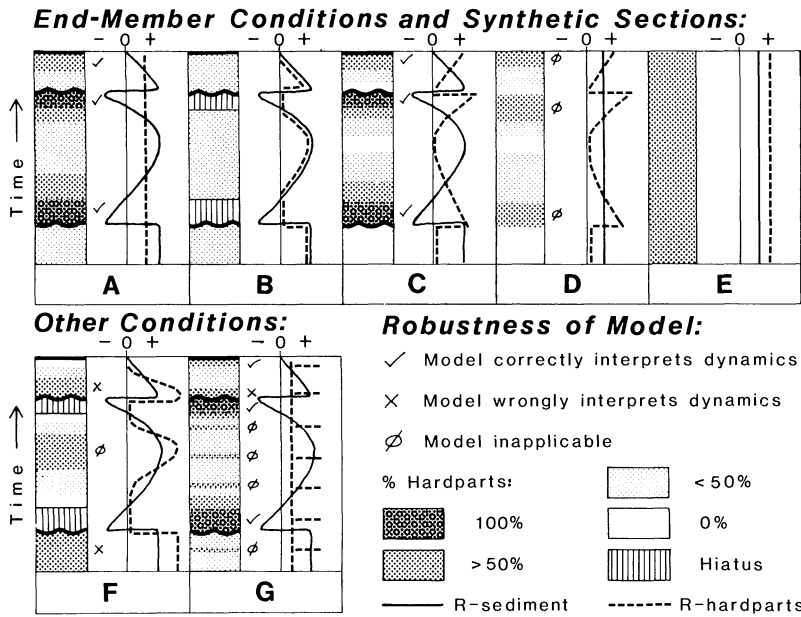
FIGURE 6. The R-sediment model is highly robust to a range of hypothetical changes in both R-hardparts and R-sediment, illustrated using synthetic stratigraphic sequences. Despite the complicated origins of some of the synthetic shell beds, the model neither rejects the R-sediment hypothesis when true nor accepts it when false in almost all examples; the conditions under which it does fail are biologically and hydraulically unlikely to arise in natural systems. Method and results explained in text.

Relaxation of assumptions

The robustness of the R-sediment model is evaluated by generating synthetic stratigraphic sequences for known, hypothetical conditions of varying hardpart input and sedimentation rate, and then scoring the model for how many of the synthetic shell beds it interprets correctly (Fig. 6). The hypothetical history of rates (volume of hardparts or sediment per unit time) is plotted to the right of each derived stratigraphic section. R-sediment is allowed to fluctuate from positive to negative values, but R-hardparts varies only from positive to zero net rates. When both R-hardparts and R-sediment are zero, a stratigraphic hiatus results (neither a sedimentary nor a hardpart record of elapsed time is preserved); omissional and erosional type discontinuities (solid flat and wavy lines, respectively) are produced when R-sediment attains zero and negative values. All relative concentrations (regardless of absolute abundance of hardparts, which is expressed as a percentage of the sediment + hardpart volume) are scored with a √ or x symbol according to whether or not the R-sediment model correctly describes the *sedimentary* dy-

namics of fossil accumulation. Hardpart concentrations that are not associated with bedding planes cannot be categorized and thus cannot be interpreted by the R-sediment model. These are scored with a phi (ϕ) symbol.

In situation A of Fig. 6, R-sediment varies against a background of constant R-hardparts. These conditions are identical to those assumed by the R-sediment model. The hypothesized fluctuations in R-sediment generate three shell beds—a Type IV, Type II, and Type I successively—and the R-sediment model for these shell bed types correctly interprets the dynamics of change in R-sediment for all three synthetic examples: the Type IV bed did form through an increase in R-sediment from an erosional to a depositional regime, etc.

The synthetic section in situation B is the product of in-phase, direct covariation of the two rates, such that R-hardparts is zero when R-sediment is zero or negative, and is positive and identical in value to R-sediment when that rate is positive. The result is a sequence consisting of beds having constant proportions of hardparts and sediment and separated by stratigraphic dis-

continuities. The fluctuations in R-sediment and R-hardparts effectively cancel each other out, so that relative concentrations of hardparts do not arise.

Section C records the opposite end-member condition in which R-hardparts varies in phase but inversely with R-sediment, so that hardpart input is highest when sedimentation rate is lowest. This pattern of covariation accentuates the stratigraphic pattern expected from variation in R-sediment alone (e.g., condition A). Even though fluctuations in hardpart input play a role in the development of each of the synthetic shell beds, the R-sediment model nonetheless correctly interprets the role of R-sediment in hardpart accumulation, and the basic taphonomic and paleobiologic predictions of the R-sediment model should still hold.

In situation D, R-sediment is constant and only R-hardparts varies. Relative concentrations of hardparts are produced by positive excursions of R-hardparts, but since sedimentation rate does not change, none of these concentrations will be associated with a stratigraphic discontinuity that permits categorization by the R-sediment model. All three concentrations "float" in a matrix of less fossiliferous sediment. The ϕ symbols indicate that the model does not apply and therefore does not lead one to wrongly accept a hypothesis of changing R-sediment.

Situation E describes a fifth end-member condition in which both R-hardparts and R-sediment are constant. The abundance of hardparts in the record is a function of the relative values of the two rates; no relative concentrations result.

Synthetic sections F and G result from more complicated dynamics of change in R-sediment and R-hardparts over time. In situation F, R-hardparts varies directly and in phase with R-sediment but ranges over different absolute values such that maximum rates of hardpart input exceed maximum rates of sedimentation. In situation G, R-hardparts maintains a constant background rate interrupted by short events of high hardpart input such as generated by mass mortality of local fauna or storm deposition of allochthonous hard parts.

Both of these hypothetical histories yield synthetic stratigraphic sequences that closely mimic real stratigraphic sequences wherein some but not all concentrations are associated with strati-

graphic discontinuities. In only three of the 11 resulting shell beds does the model fail to correctly interpret the sedimentary dynamics of accumulation. In each of these cases, the high rate of hardpart input responsible for the failure is biologically or hydraulically unlikely since it must occur when sedimentation is similarly high. High rates of sedimentation are inimical to most benthos and especially suspension feeders, which are major hardpart producers by virtue of their typically larger body sizes and/or large population sizes and rapid turnover rates as compared to skeletonized deposit feeders and taxa from higher trophic levels. Continuously high rates of sedimentation and frequent episodes of rapid sedimentation increase the danger of catastrophic burial, clogging of filtering apparatus, self-silting with pseudofeces, and foundering of both larvae and adults in soupy substrata (Lund 1957; Kranz 1974; Thayer 1975; Gerrodette and Flechsig 1979).

Usually, hardparts behave differently from non-bioclastic sediment by virtue of shape, size, and specific density differences, all of which affect critical threshold velocities of particle erosion and deposition (Johnson 1957; Middleton 1967). The hydraulic injection of hardparts is most likely to be high when sedimentation rates are low unless the hardparts are hydraulically equivalent to the sediment matrix (e.g., microfossils in fine sands and muds; macroinvertebrates in coarse sands and gravels). Macroinvertebrate skeletal elements in sandy and finer-grained sediments will be among the first particles to settle on a discontinuity surface out of either suspension or bedload transport, and hardparts set in motion by local reworking or in transport from allochthonous sources will cause R-hardparts to be high when R-sediment is low. This behavior is implicit in regular size sorting of large hardparts up into finer sediment within shelly storm lags and turbidites. It will not occur if the capacity of the transporting agent is so overwhelmed by sediment supply that all particles are deposited immediately and without opportunity for sorting, or if hardparts and sediment are hydraulically equivalent. In these situations, however, the hardparts should not be concentrated along a single discontinuity surface but should instead be dispersed throughout the sedimentation unit or be concentrated at some level within it—the

shells will be found within the bed rather than concentrated along its upper or lower contact. The model cannot mistakenly interpret such concentrations since they cannot be categorized as Type I, II, III, or IV.

To summarize, the R-sediment model appears to be robust to relaxation of the unrealistic assumption of constant hardpart input. Concentrations formed by fluctuations in R-hardparts alone should not be associated with stratigraphic discontinuities, and where both R-hardparts and R-sediment are factors, the R-sediment model still correctly interprets the sedimentary dynamics of formation and thus its taphonomic and paleobiologic predictions should still hold.

Robustness to complex changes in R-sediment

A second assumption of the model is that changes in R-sediment are always gradual and monotonic. The consequences of more variable patterns of change in sedimentation are evaluated in Fig. 7 by holding R-hardparts constant. The synthetic section is generated using the same procedure as for Fig. 6; inflection points in the hypothetical R-sediment curve are numbered sequentially for identification.

In the hypothetical R-sediment history, the abrupt drop in net sedimentation from point 1 to 2 (and from point 3 to 4) occurs so rapidly that no appreciable hardpart record of the change arises: the expected Type I and II shell beds do not develop. In contrast, when R-sediment increases rapidly from an interval of zero or negative net sedimentation, a shell bed can arise during the interval of low net sedimentation (Type III or IV in features). The rapid shift to high R-sediment (for example, from point 2 to 3) simply abbreviates the upper part of the shell bed that might have formed had R-sediment changed more gradually. The concentration will grade rapidly or be sharply capped by overlying less fossiliferous sediments. If the increase in R-sediment is very rapid, the concentration will consist of a single fossil assemblage that is taphonomically and ecologically homogeneous because of insufficient time for selective destruction and colonization of hardparts. In the stratigraphic record, numerous examples of thin, rapidly gradational Type III and IV concentrations are provided by sediment-capped storm lags, shelly turbidites, and mud-smothered colonists of firm-

grounds and hardgrounds, and these are typified by taphonomically undifferentiated fossil assemblages (e.g., single event, rapidly buried tempestites of Aigner et al. 1978; Aigner 1982).

Short-term oscillations or reversals in sedimentation rate will characterize longer intervals of steady or slowly changing R-sediment. These R-sediment trends will produce accumulations having complex internal stratigraphies created by the physical amalgamation or more passive condensation of many small-scale/short-term concentrations. The overall increase in R-sediment between points 4 and 13 in Fig. 7 generates a Type IV concentration that has an erosional base and grades upward into less fossiliferous sediment, but in detail it consists of a series of smaller-scale concentrations produced and amalgamated to varying degrees by short-term negative excursions in R-sediment. Short-term concentrations in the lower part of the complex Type IV deposit will suffer more amalgamation and reworking than those in the upper part, and will typically be Type II and IV erosional concentrations rather than the Type I and III omissional concentrations such as found higher in the deposit. The complex Type IV shell bed should thus exhibit the general expected trends in postmortem bias and biotic response to hardpart accumulation despite the nonmonotonic history of R-sediment. However, assemblages sampled at successive horizons within such complex deposits would have to be evaluated taphonomically in terms of their short-term dynamics of accumulation as well as within the context of the longer-term R-sediment history.

Back-to-back monotonic changes in R-sediment provide another complex R-sediment condition for hardpart accumulation, and create concentrations that in structure and dynamics are the composite of two different kinds of shell beds. A decrease in R-sediment to zero net sedimentation followed by a gradual increase (point 13 to 15 in Fig. 7) yields a Type I concentration overlain directly by a Type III. The composite shell bed has gradational lower and upper contacts and is divided by a shared omission discontinuity (see also composite I–III bed formed by a shorter-term fluctuation in R-sediment between points 9 and 11). Composite Type II–IV beds are produced when the excursion in R-sediment attains negative values; these beds are

SYNTHETIC
STRATIGRAPHIC
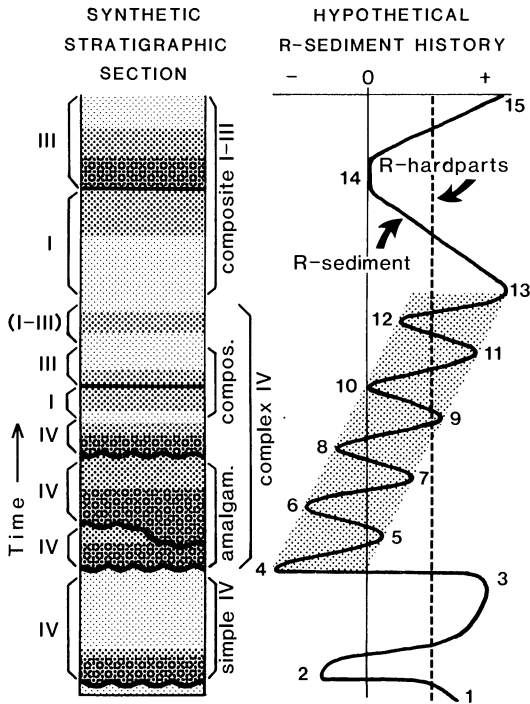SECTION

HYPOTHETICAL
R-SEDIMENT HISTORY

FIGURE 7.   Step-wise changes in net sedimentation and the superposition of short-term oscillations on monotonic trends produce more complicated patterns of fossil abundance, which mimic closely those found in the Miocene study area.

characterized by an internal erosion surface. In composite deposits, the predicted taphonomic and paleobiologic trends combine those of the component shell bed types. Composite II–IV shell beds are expected to be infrequent in the stratigraphic record because of the problem of erosional reworking of the Type II bed. This increases the likelihood that when Type IV shell beds are encountered in the record, their assemblages will contain hardparts of mixed origin and different states of preservation.

Composite shell beds in which both upper and lower contacts are sharp are also possible although not illustrated in Fig. 7. Good examples are provided in the stratigraphic record by storm lags and Type III condensed beds that are not covered immediately by sediment but are smothered catastrophically at some later time, producing composite Type IV-I, IV-II, III-I, and III-II concentrations depending on the energy of the depositional event.

In the hypothetical sequence illustrated in Fig. 7, the model fails to identify shell bed 12 as sedimentologic in origin. The concentration lacks any sharp contact (internal or external) because

R-sediment does not actually attain zero or negative values, and so the bed cannot be categorized and analyzed by the model.

Expected operation under other conditions

The discussion of the model implies that hardparts are supplied from local production (i.e., are autochthonous) of marine benthic macroinvertebrates in a terrigenous depositional system. The model should apply to other conditions.

Nektic and allochthonous benthic hardpart supply.—The introduction of allochthonous and nektic macroinvertebrate hardparts will not interfere with the development of expected trends in post-mortem bias, and taphonomic feedback should proceed since the living organisms are responding to the physical presence of hardparts in the substratum, not to their ultimate source or ecological role in some former community. Because the supply of nektic hardparts can vary completely independently of sedimentation rate, it is hypothetically possible to produce concentrations that invalidate the model (such as the upper shell bed in Fig. 6F). However, given the episodic nature of sedimentation itself (e.g., Barrell 1917; Tipper 1983), brief pulses of high hardpart input such as from mass mortalities of nekton have a higher probability of coinciding with intervals of nondeposition than with very brief and sporadic conditions of sediment aggradation, even if hardpart pulses are timed randomly.

Plankton and reworked microfossils.—Input of pelagic microfossils can also be independent of benthic sedimentation events. If this input is constant, the system behaves under the idealized conditions of the initial model; variations in R-hardparts result in the same patterns of skeletal abundance and model robustness as already discussed in Fig. 6. Because of the small size of the bioclasts, taphonomic feedback in the benthic community will be subtle or absent—although the mass properties of globigerine sediments should differ from pelagic clays—and the trends in abrasion, bioerosion, etc., would depend upon the susceptibility of the dead tests to local processes of skeletal destruction. The most complicated deviation from the model results when microfossils are hydraulically equivalent to the terrigenous sediment and are supplied as allochthonous, reworked material in bedload. This

sets up a dependent rate relationship in which total hardpart supply will be highest when R-sediment is highest (either situation B or F in Fig. 6). Whether or not a relative concentration of fossils results will depend on how rates of hardpart destruction at the accumulation site (and thus net hardpart input) vary with R-sediment.

Vertebrates.—In vertebrate accumulations, net hardpart input might actually drop off quickly when R-sediment is low, because prefossilization appears to be essential to successful reworking of hardparts. This is a complication in dependent rate relationships, however, not in the fundamental validity of the R-sediment model, and points out potential threshold effects to be considered when making taphonomic comparisons across major taxonomic groups. In marine settings, vertebrate material should offer opportunities at least for facilitative taphonomic feedback that are similar to those provided by macroinvertebrate hardparts (for example, colonization of relict bones by pholad bivalves and barnacles, Frey et al. 1975).

Other depositional systems.—The R-sediment model should apply equally well to carbonate depositional systems, although not without pitfalls. Primary depositional contacts of shell beds in limestone sequences, for example, are readily obscured through diagenesis, which can both obliterate initially sharp contacts (e.g., pervasive dolomitization, recrystallization) and sharpen initially gradational contacts (e.g., pressure solution). In addition, operational definitions that distinguish between sediment and hardparts are required since bioclast disintegration and biologically mediated precipitation figure so largely in carbonate rock genesis. The R-sediment model should also work in terrestrial depositional systems, although the specific processes responsible for changes in net sedimentation are different. Type I and rarely Type II concentrations are indicated for bone and floral concentrations in paleosols, and Type III and IV concentrations will be represented by skeletal concentrations along bedding planes within point bars and by channel lags.

Application to the fossil record

There are several pitfalls to direct application of the R-sediment model in the stratigraphic record.

1. Bioturbation and diagenesis can obliterate evidence of an initially sharp contact, so that a concentration cannot be evaluated by the model even though it is sedimentologic in origin. This leads to a conservative error: the model would lead the investigator to underestimate the number of sedimentologic concentrations in the study area and thus cause the rejection of potentially comparable paleontologic samples.

2. Alternatively, sharp contacts can be produced post-depositionally by diagenesis (pressure solution within carbonate sequences, compaction of shaley partings in terrigenous sequences) and by living organisms. Biogenic contacts, such as the sharp irregular surfaces associated with feeding pits and *Arenicola*-graded beds, can be recognized on the basis of overall form (topography) and lateral extent of the surface, and environmental context (e.g., *Arenicola*-graded beds are known only from intertidal settings; Rhoads and Stanley 1965; Cadée 1976). Fossil concentrations that fill burrows in firmgrounds do not present a problem because these burrowed surfaces are formed during intervals of low net sedimentation (either following autocompaction of mud at the seafloor, or erosional exhumation of mud compacted through burial), and thus are consistent with the model's presumption that sharp contacts indicate discontinuities in sediment deposition. In lithified sediments, the diagenetic significance of sharp contacts is evaluated petrographically on a case-by-case basis, but the original nature of some sharp contacts will probably be indecipherable.

3. Not all intervals of relatively low net sedimentation produce discontinuity surfaces. When background rates of hardput input are high, slight slowdowns in net sedimentation can result in a relative concentration of fossil material without an episode of true erosion or omission (e.g., bed 12 in Fig. 7). The model will fail to recognize these concentrations as sedimentologic in origin using the bed contact criterion, even though other criteria such as winnowed matrix, hydraulically reoriented shells, and glauconite grains might indicate an episode of reduced net sedimentation. Field experience suggests that bedding surfaces are best developed in sequences composed of sediment ranging down to clay- and silt-sized material.

4. Distinguishing omission surfaces from ero-

sional surfaces can be difficult in the field. Although this pitfall does not undermine the validity of the approach, it does limit how precisely the model can be applied to the interpretation of particular shell or bone beds. Positive evidence for erosion includes truncation of underlying structures, scour-shaped irregularities of the surface, and the incorporation of rip-ups from older deposits, in order of decreasing confidence. Omission, on the other hand, is simply the condition of no net deposition; omission surfaces are characterized by low topographic relief, burrows or borings into older deposits, a concentration of glauconitic or phosphatic authigenic minerals, and mineralization or other cementation of underlying sediments.

Any of the omission features can characterize erosion surfaces, and in fact can obliterate evidence for the initial erosional origin of the surface. In the field, I categorize a surface as erosional if it has any indication of being erosional during its history, and categorize all other surfaces as omission types. Using this operational definition, some omission surfaces may well be incorrectly identified as erosional, for example, if omission was characterized by dynamic bypassing, and some erosional surfaces will be misidentified as omission surfaces. However, from the perspective of sedimentary dynamics as well as taphonomic history of the fossil assemblages, the most important distinction is between Type I and II beds on the one hand and Type III and IV beds on the other—that is, between the roof beds and the sole beds—and distinctions within these categories are desirable but not critical to the phrasing of reasonable and testable taphonomic hypotheses using the model.

The practical utility of the model—both as a means of interpreting modes of fossil concentration and as a guide to paleontologic sampling—remains to be tested in the field. Largely qualitative observations in the Maryland Miocene study area indicate that shell beds that can be categorized as Type I–IV on the basis of bed contacts (1) exhibit independent sedimentologic evidence of accumulation during conditions of relatively low net sedimentation, and (2) exhibit some if not all of the taphonomic and paleobiologic features predicted by the R-sediment model (Kidwell, in prep., data in Kidwell 1982a). In general, the development of expected

trends depends most upon the time interval of hardpart accumulation within these shallow-water (middle shelf to intertidal), open to marginal marine fine sands and muds (see Gernant [1971] and Kidwell [1984] for paleoenvironmental analyses).

For example, small-scale Type I-IV concentrations that were formed relatively rapidly by storms, by bottom scavengers and predators, and by the lateral migration of channels and fair-weather bedforms contain fossil assemblages that are homogeneous in composition and in physical condition throughout the thickness of the individual shell bed. Out of the dozens of small-scale concentrations examined in each of 194 stratigraphic sections of the Maryland Miocene, only one showed good evidence of taphonomic feedback: a Type II winnowed lag of infaunal *Turritella* gastropods encrusted by a multilayered, continuous sheet of bryozoans (Kidwell and Jablonski 1983).

In contrast, expected trends are well developed in the four large-scale Miocene fossil concentrations, which accumulated during prolonged regimes (thousands of years to ten thousand years) of low net sedimentation during successive transgressions (Kidwell 1982b, 1984). These internally complex, Type IV beds each consist of a fragmental shell hash resting on the basal disconformity, a middle interval of densely packed, disarticulated whole and broken shells, and an upper subunit of physically amalgamated but individually distinguishable shell horizons containing larger proportions of articulated and unbroken specimens (Kidwell 1982a; Kidwell and Jablonski 1983; Kidwell, in prep.). These features are consistent with the taphonomic predictions of the R-sediment model for Type IV shell beds, in which frequency and intensity of post-mortem fragmentation and physical amalgamation and time averaging of assemblages decreases upward. A tally of the frequency of bored and encrusted shells in three exposures of one of the major shell beds of the Choptank Formation indicates a statistically significant decrease from 12% in the most densely packed parts of the bed to less than 1% in shell-poor horizons (combined $N = 8,142$ for 8 samples), and a more extensive faunal survey of this same bed demonstrates a significant correlation between the relative abundance of shell-gravel taxa (fouling

organisms, epifauna, shallow infauna with modern congeners tolerant or preferring shell gravel substrata) and shell packing density (unpub. data from Kidwell, in prep.). Alternative explanations of this correlation in assemblage composition and shell-packing density can be rejected. The similar sedimentary matrix of the samples argues against changing water depth or energy, and the assemblages do not appear to be the product of mixing of autochthonous and allochthonous material. Significant transport of hardparts is probably excluded by the poor size and shape sorting of hardparts, lack of association with high-energy sedimentary structures, and absence of appropriate kinds of fossils in adjacent sedimentary facies to have provided source material (Kidwell and Jablonski 1983). Finally, some minor morphologic fluctuations in the bivalve species *Lucina anodonta* and seven other molluscs in the Maryland Miocene (Kelley 1979, 1983a, b) coincide with changes in shell-packing density through the stratigraphic sequence, and thus might be ecophenotypic in origin (Kidwell and Aigner 1985). This would lend further support for Kelley's interpretation of evolutionary stasis within these species.

Conclusions

The R-sediment model represents a heuristic analysis of the taphonomic and paleobiologic consequences of only one factor in fossil concentrations—sedimentation rate. Despite its radical reduction of variables in the formation of a fossil record, the model is highly robust as illustrated by its ability to correctly explain shell beds produced under realistic, hypothetical conditions. More importantly, it predicts a broad spectrum of taphonomic phenomena including little-appreciated ecological interactions between living communities and dead hardparts. Although this paper stresses marine macroinvertebrate concentrations, the model should theoretically apply to vertebrate, microfossil, and terrestrial concentrations as well.

1. One immediate conclusion of the model is that fossil-rich and fossil-poor intervals of the stratigraphic record are qualitatively different, both as repositories of paleontologic information and as settings for biotic interactions. Densely fossiliferous strata have greater probability of post-mortem bias from selective hardpart de-

struction and time averaging. In addition, they present probably unique opportunities for live: dead interactions, which influence the ecological and morphometric composition of fossil assemblages by bringing about directional changes in the structure of benthic communities.

2. The usefulness of the model in the interpretation of the fossil record has been evaluated only qualitatively, and in relatively few settings. However, the prospects are reasonably good. One advantage of the model is its use of a very simple, descriptive criterion—bed contacts—which can generally be evaluated in the field with some confidence. On this basis, the model generates a testable hypothesis for the mode of formation of the concentration, the kinds and levels of bias within its fossil assemblages, and biotic interactions between dead hardparts and the living community. The model indicates that samples collected from one part of a shell bed are not necessarily equivalent, either taphonomically or paleobiologically, to samples collected at other horizons within that bed, and that both paleoecological and evolutionary studies that depend upon data collected serially through stratigraphic sequences need to consider the sedimentary dynamics that can underlie variations in fossil abundance.

3. Regardless of whether the R-sediment hypothesis is accepted or rejected for a particular fossil bed—or rather, regardless of the extent to which factors other than sedimentation are found to have influenced the concentration—the model provides a departure point for analysis. By using the predictions of the R-model as a baseline for the effects of changes in net sedimentation, the paleontologist can recognize contradictory trends which must indicate other factors such as (a) insufficient time for differential destruction of hardparts or for their colonization by living benthos, (b) environmental conditions which excluded bioeroders or benthos in general, and (c) hydraulic equivalence between hardparts and embedding matrix. Even concentrations which are not associated with stratigraphic discontinuities can be evaluated from this perspective.

4. By concentrating on the underlying change in sedimentation rate rather than on the vast array of processes that can cause such changes, the model promotes comparison of assemblages of different ages and taxonomic compositions and

across environmental gradients. Detailed ecological and evolutionary comparisons become feasible if a single type of shell bed is sampled throughout. For example, a transect based on erosive washover deposits, swash zone shell laminae, lags produced by channel and shoal migration, inner shelf storm concentrations, and shelly proximal turbidites (which are all comparably short-term Type IV concentrations) should yield assemblages that are taphonomically more comparable to each other than to assemblages from short-term Type I, II, or III concentrations. The R-sediment model also yields larger-scale predictions for the nature and distribution of fossil concentrations (Kidwell, in prep.). For example, as a function of sedimentary dynamics, post-mortem bias should vary not only among environments, but also among assemblages accumulated during different phases of basin history (e.g., sediment starvation during rapid sea-level rise versus rapid sediment accumulation with progradation during stillstand) and in different tectonic settings and latitudes (cratonic vs. rapidly subsiding active margins; seasonal variation vs. constant rates of sediment supply, hardpart production, and hardpart preservation potential). These predictions have application to sedimentologic and stratigraphic analysis of the record as well as to paleobiologic studies (Kidwell, 1985).

5. Finally, the R-sediment model is not a general model, despite its predictive powers: many shell and bone concentrations cannot be addressed because they lack sharp contacts, or because the origin of those contacts is unclear. However, as an exercise, the R-sediment model reveals the heuristic value of forward modeling methods to taphonomic analysis, and suggests by its power and robustness that R-sediment may well be a primary control on the nature of the fossil record. An alternative model in which sedimentation rates are held constant and only the rate of hardpart input varies produces shell-rich and shell-poor strata, as illustrated in Fig. 6D, but this model does not predict taphonomic bias or biotic interactions. This is because rates of hardpart input do not govern individual hardpart residence time at the depositional interface, and have little direct influence on sedimentation rates or sedimentary dynamics. The R-hardparts

model thus has little predictive power compared to the power that the R-sediment model holds.

As a working hypothesis, then, sedimentation rather than hardpart input appears to be the primary control on the nature of the fossil record, determining when, where, and how hardparts can accumulate into fossiliferous deposits. From this perspective, the biological and diagenetic factors governing net hardpart input play a secondary role, determining which of the many potential R-sediment concentrations will actually be realized in the stratigraphic record and how well the expected taphonomic and paleobiologic features of those concentrations will be developed. Episodes of low net sedimentation cannot concentrate fossils in the absence of hardpart input, as reflected in the many unfossiliferous unconformities and bedding planes in the record. A systematic exploration of how R-sediment and R-hardparts vary (and covary) as a function of environment, latitude or climatic regime, tectonic setting, matrix composition (carbonate vs. terrigenous), taxonomic group, and geologic age will be essential to quantitative modeling and testing of these ideas. But at present, this ranking of controlling factors appears to be considerably more powerful than the more familiar approaches emphasizing hardpart input.

Acknowledgments

Literature Cited

AIGNER, T. 1982. Calcareous tempestites: storm-dominated stratification in upper Muschelkalk limestones (Triassic, SW-Germany). Pp. 180–198. In: Einsele, G. and A. Seilacher, eds. Cyclic and Event Stratification. Springer-Verlag; Berlin.

AIGNER, T., H. HAGDORN, AND R. MUNDLOS. 1978. Biohermal,

biostromal and storm-generated coquinas in the Upper Muschelkalk. N. Jb. Geol. Paläontol. Abh. *157*:42–52.

AIGNER, T. AND H.-E. REINECK. 1982. Proximality trends in modern storm sands from the Helgoland Bight (North Sea) and their implications for basin analysis. Senckenberg. Marit. *14*:183–215.

ALEXANDERSSON, T. 1972. Micritization of carbonate particles: processes of precipitation and dissolution in modern shallow-marine sediments. Bull. Geol. Inst. Univ. Uppsala N.S. *3* (7): 201–236.

ALEXANDERSSON, T. 1978. Destructive diagenesis of carbonate sediments in the eastern Skagerrak, North Sea. Geology. *6*:324–327.

ALLER, R. C. 1982. Carbonate dissolution in nearshore terrigenous muds: the role of physical and biological reworking. J. Geol. *90*: 79–95.

ANDERSON, T. F., M. L. BENDER, AND W. S. BROECKER. 1973. Surface areas of biogenic carbonates and their relation to fossil ultrastructure and diagenesis. J. Sed. Petrol. *43*:471–477.

BARRELL, J. 1917. Rhythms and the measurement of geologic time. Geol. Soc. Am. Bull. *28*:745–904.

BEHRENSMEYER, A. K. 1978. Taphonomic and ecologic information from bone weathering. Paleobiology. *4*:150–162.

BEHRENSMEYER, A. K. AND A. P. HILL, EDS. 1980. Fossils in the Making: Vertebrate Taphonomy and Paleoecology. Univ. Chicago Press; Chicago.

BRETT, C. E. AND M. E. BROOKFIELD. 1984. Morphology, faunas, and genesis of Ordovician hardgrounds from southern Ontario, Canada. Palaeogeogr., Palaeoclim., Palaeoecol. *46*:233–290.

BRINKMANN, R. 1929. Statistisch-biostratigraphische Untersuchungen an mitteljurassischen Ammoniten über Artbegriff und Stammesentwicklung. Abh. Ges. Wiss. Göttingen, Math.-Phys. Kl., N.F., *13*:249 pp.

CADÉE, G. C. 1968. Molluscan biocoenoses and thanatocoenoses in the Ria de Arosa, Galicia, Spain. Zool. Verhandl. Rijkmus. Nat. Hist. Leiden. *95*:1–121.

CADÉE, G. C. 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res. *10*:440–460.

CADÉE, G. C. 1979. Sediment reworking by the polychaete *Heteromastus filiformis* on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. *13*:441–456.

CAMPBELL, C. V. 1967. Lamina, laminaset, bed and bedset. Sedimentology. 8:7–26.

CARTER, R. W. G. 1974. Feeding sea birds as a factor in lamellibranch valve sorting patterns. J. Sed. Petrol. *44*:689–692.

CHAVE, K. E. 1964. Skeletal durability and preservation. Pp. 377–387. In: Imbrie, J. and N. D. Newell, eds. Approaches to Paleoecology. Wiley; New York.

CRISP, D. J. 1976. Settlement responses in marine organisms. Pp. 83–124. In: Newell, R. C., ed. Adaptations to Environment: Essays on the Physiology of Marine Animals. Butterworths; London.

DRISCOLL, E. G. 1967. Experimental field study of shell abrasion. J. Sed. Petrol. *37*:1117–1123.

DRISCOLL, E. G. 1970. Selective bivalve shell destruction in marine environments: a field study. J. Sed. Petrol. *40*:898–905.

DRISCOLL, E. G. AND T. P. WELTIN. 1973. Sedimentary parameters as factors in abrasive shell reduction. Palaeogeogr. Palaeoclimatol. Palaeoecol. *13*:275–288.

DRISCOLL, E. G., R. A. SWANSON, AND J. SULANOWSKI. 1974. Seasonal variations in sedimentary carbonate. Geol. Soc. Am. Abstr. *6*:1034–1036.

ELLER, M. G. 1981. The Red Chalk of eastern England: A Cretaceous analogue of Rosso Ammonitico. Pp. 207–231. In: Farinacci, A. and S. Elmi, eds. Rosso Ammonitico Symp. Proc. Ed. Technoscienza; Rome.

FAGERSTROM, J. A. 1964. Fossil communities in paleoecology: their recognition and significance. Geol. Soc. Am. Bull. *75*:1197–1216.

FLESSA, K. W. AND T. J. BROWN. 1983. Selective solution of macroinvertebrate calcareous hard parts: a laboratory study. Lethaia. *16*:193–205.

FORCE, L. M. 1969. Calcium carbonate size distribution on the West Florida shelf and experimental studies on the microarchitectural control of skeletal breakdown. J. Sed. Petrol. *39*:902–934.

FREY, R. W., M. R. VOORHIES, AND J. D. HOWARD. 1975. Estuaries of the Georgia Coast, U.S.A.: Sedimentology and Biology. VIII. Fossil and recent skeletal remains in Georgia estuaries. Senckenbergiana Marit. 7:257–295.

FÜRSICH, F. T. 1979. Genesis, environments, and ecology of Jurassic hardgrounds. N. Jb. Geol. Paläontol. Abh. *158*:1–63.

FÜRSICH, F. T. AND E. G. KAUFFMAN. 1984. Palaeoecology of marginally marine sedimentary cycles in the Albian Bear River Formation of southwestern Wyoming (USA). Palaeontology. *27*: 501–536.

FUTTERER, D. K. 1974. Significance of the boring sponge *Cliona* for the origin of fine grained material of carbonate sediments. J. Sed. Petrol. *44*:79–84.

FUTTERER, E. 1978a. Studien uber die Einregelung, Anlagerung und Einbettung biogener Hartteile im Stromungskanal. N. Jb. Geol. Paläontol. Abh. *156*:87–131.

FUTTERER, E. 1978b. Hydrodynamic behavior of biogenic particles. N. Jb. Geol. Paläontol. Abh. *157*:37–42.

GERNANT, R. E. 1971. Invertebrate biofacies and paleoenvironments. Pp. 19–30. In: Gernant, R. E., T. G. Gibson, and F. C. Whitmore, Jr., eds. Environmental History of Maryland Miocene. Maryland Geol. Survey Guidebook No. 3; Baltimore.

GERRODETTE, T. AND A. O. FLECHSIG. 1979. Sediment-induced reduction in the pumping rate of the tropical sponge *Verongia lacunosa*. Mar. Biol. *55*:103–110.

GOLUBIC, S., R. D. PERKINS, AND K. J. LUKAS. 1975. Boring microorganisms and microborings in carbonate substrates. Pp. 229–259. In: Frey, R. W., ed. The Study of Trace Fossils. Springer-Verlag; New York.

HEIM, A. 1924. Über submarine Denudation und chemische Sedimente. Geol. Rundsch. *15*:1–47.

HEIM, A. 1958. Oceanic sedimentation and submarine discontinuities. Eclogae Geol. Helvet. *51*:642–649.

HILL, G. W., K. A. ROBERTS, J. L. KINDINGER, AND G. D. WILEY. 1982. Geobiologic study of the south Texas outer continental shelf. U.S. Geol. Survey Prof. Pap. 1238: 36 pp.

HOLLMAN, R. 1968. Zur Morphologie rezenter Mollusken-Bruchschille. Paläontol. Z. *42*:217–235.

JENKYNS, H. C. 1971. The genesis of condensed sequences in the Tethyan Jurassic. Lethaia. *4*:327–352.

JERVEY, M. T. 1974. Transportation and dispersal of biogenic material in the nearshore marine environment. Unpub. Ph.D. diss., Louisiana St. Univ., 340 pp.

JOHNSON, R. G. 1957. Experiments on the burial of shells. J. Geol. *65*:527–535.

JOHNSON, R. G. 1960. Models and methods for analysis of the mode of formation of fossil assemblages. Geol. Soc. Am. Bull. *71*:1075–1088.

JUMARS, P. A. AND A. R. M. NOWELL. 1984. Fluid and sediment dynamic effects on marine benthic community structure. Am. Zool. *24*:45–55.

KELLEY, P. H. 1979. Mollusc lineages of the Chesapeake Group (Miocene). Unpub. Ph.D. diss., Harvard Univ., 220 pp.

KELLEY, P. H. 1983a. Evolutionary patterns of eight Chesapeake Group molluscs: Evidence for the model of punctuated equilibria. J. Paleontol. *57*:581–598.

KELLEY, P. H. 1983b. The role of within-species differentiation

in macroevolution of Chesapeake Group bivalves. Paleobiology. 9:261–268.

KIDWELL, S. M. 1982a. Stratigraphy, invertebrate taphonomy and depositional history of the Miocene Calvert and Choptank Formations, Atlantic Coastal Plain. Unpub. Ph.D. diss, Yale Univ., 514 pp.

KIDWELL, S. M. 1982b. Time scales of fossil accumulation: Patterns from Miocene benthic assemblages. 3d N. Am. Paleontol. Conv., Proc. 1:295–300.

KIDWELL, S. M. 1984. Outcrop features and origin of basin margin unconformities, Miocene Lower Chesapeake Group, Atlantic Coastal Plain. Am. Assoc. Petrol. Geol. Mem. 37:37–58.

KIDWELL, S. M. 1985. Palaeobiological and sedimentological implications of fossil concentrations. Nature 318:457–460.

KIDWELL, S. M. AND T. AIGNER. 1985. Sedimentary dynamics of complex shell beds: implications for ecologic and evolutionary patterns. Pp. 382–395. In: Bayer, U. and A. Seilacher, eds. Sedimentary and Evolutionary Cycles. Springer Verlag; Berlin.

KIDWELL, S. M. AND D. JABLONSKI. 1983. Taphonomic feedback: Ecological consequences of shell accumulation. Pp. 195–248. In: Tevesz, M. J. S. and P. L. McCall, eds. Biotic Interactions in Recent and Fossil Benthic Communities. Plenum; New York.

KRANZ, P. M. 1974. The anastrophic burial of bivalves and its paleoecological significance. J. Geol. 82:237–265.

LEVER, J. 1958. Quantitative beach research. I. The "left-right phenomenon": sorting of lamellibranch valves on sandy beaches. Basteria. 22:21–51.

LEVER, J., A. KESSLER, A. P. VAN OVERBEEKE, AND R. THIJSSEN. 1961. Quantitative beach research. II. The "hole effect" a second mode of sorting of lamellibranch valves on sandy beaches. Neth. J. Sea Res. 1:339–358.

LEVER, J. AND R. THIJSSEN. 1968. Sorting phenomena during the transport of shell valves in sandy beaches studied with the use of artificial valves. Symp. Zool. Soc. London. 22:259–271.

LEWY, Z. 1975. Early diagenesis of calcareous skeletons in the Baltic Sea, western Germany. Meyniana. 27:29–333.

LINDBERG, D. R. AND M. G. KELLOGG. 1982. Bathymetric anomalies in the Neogene fossil record: The role of diving marine birds. Paleobiology 8:402–407.

LUND, E. J. 1957. Self-silting by the oyster and its significance for sedimentation geology. Univ. Tex. Contrib. Mar. Sci. 4:320–327.

McCARTHY, B. 1979. Trace fossils from a Permian shoreface-foreshore environment, eastern Australia. J. Paleobiol. 53:345–366.

MIDDLETON, G. V. 1967. The orientation of concavo-convex particles deposited from experimental turbidity currents. J. Sed. Petrol. 37:229–232.

MOORE, H. B. 1972. An estimate of carbonate production by macrobenthos in some tropical soft-bottom communities. Mar. Biol. 17:145–148.

MÜLLER, A. H. 1976. Lehrbuch der Paläozoologie, Band I Allgemeine Grundlagen. Fischer; Jena. 423 pp.

MÜLLER, A. H. 1979. Fossilization (Taphonomy). Pp. A2–A78. In: Robison, R. A. and C. Teichert, eds. Treatise on Invertebrate Paleontology, Part A. Allen Press; Lawrence, Kansas.

NOWELL, A. R. M. AND P. A. JUMARS. 1984. Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst. 15:303–328.

PETERSON, C. H. 1976. Relative abundances of living and dead molluscs in two California lagoons. Lethaia. 9:137–148.

PFANNKUCHE, O., R. THEEG, AND H. THIEL. 1983. Benthos activity, abundance and biomass under an area of low upwelling off Morocco, northwest Africa. "Meteor" Forsch.-Ergebnisse D 36: 85–96.

PROBERT, P. K. 1984. Disturbance, sediment stability, and trophic structure of soft-bottom communities. J. Mar. Res. 42:893–921.

RHOADS, D. C. 1967. Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. J. Geol. 75:461–476.

RHOADS, D. C. 1970. Mass properties, stability, and ecology of marine muds related to burrowing activity. Pp. 391–406. In: Crimes, T. P. and J. C. Harper, eds. Trace Fossils. Seel House Press; Liverpool.

RHOADS, D. C. AND D. J. STANLEY. 1965. Biogenic graded bedding. J. Sed. Petrol. 35:956–963.

SCHÄFER, W. 1972. Ecology and Palaeoecology of Marine Environments (I. Oertel, transl.). Univ. Chicago Press; Chicago. 568 pp.

SEPKOSKI, J. J., JR. 1978. Taphonomic factors influencing the lithologic occurrence of fossils in Dresbachian (Upper Cambrian) shaley facies. Geol. Soc. Am. Abstr. 10:490.

SYLVESTER-BRADLEY, P. C. 1977. Biostratigraphical tests of evolutionary theory. Pp. 41–63. In: Kauffman, E. G. and J. E. Hazel, eds. Concepts and Methods of Biostratigraphy. Dowden, Hutchinson & Ross; Stroudsburg, Pa.

TAYLOR, J. D. AND M. LAYMAN. 1972. The mechanical properties of bivalve (Mollusca) shell structures. Palaeontology. 15:73–87.

THAYER, C. W. 1975. Morphological adaptations of benthic invertebrates to soft substrata. J. Mar. Res. 33:177–189.

TIPPER, J. C. 1983. Rates of sedimentation and stratigraphic completeness. Nature. 302:696–698.

WALKER, K. R. AND L. P. ALBERSTADT. 1975. Ecological succession as an aspect of structure in fossil communities. Paleobiology. 1:238–257.

WANLESS, H. R. 1979. Limestone response to stress: Pressure solution and dolomitization. J. Sed. Petrol. 59:437–462.

WARME, J. E. 1975. Borings as trace fossils, and the processes of marine bioerosion. Pp. 181–227. In: Frey, R. W., ed. The Study of Trace Fossils. Springer-Verlag; New York.

WHEELER, H. E. 1964. Baselevel, lithosphere surface, and time-stratigraphy. Geol. Soc. Am. Bull. 75:599–610.

WILLIAMSON, P. G. 1981. Palaeontological documentation of speciation in Cenozoic molluscs from Turkana Basin. Nature. 293: 437–443.

WILLIAMSON, P. G. 1982. Punctuationism and Darwinism reconciled? Nature. 296:611–612.