Sequence Stratigraphy, Paleoecology, and Evolution: Biotic Clues and Responses to Sea-Level Fluctuations

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Paleoecology has a dual relationship with sequence stratigraphy. On one hand, body and trace fossils, together with their taphonomy, may provide sensitive indicators of environmental parameters, including depth, substrate consistency, sedimentation rate/turbidity, and benthic oxygenation, which are critical in recognizing and interpreting parasequences and sequences. Fossils may provide some of the best guides to identifying key surfaces and inferring sedimentation dynamics within sequences. Conversely, the sequence stratigraphic paradigm and its corollaries provide a predictive framework within which to examine biotic changes and interpret their probable causes. Such changes include ecological epiboles (short-term, widespread proliferation of normally rare species), outages (absence of normally common species), ecophenotypic changes, and long-term (tens to hundreds of Ka) community replacement. Community replacement should be carefully distinguished from short-term (10 to a few hundred years) ecological succession, rarely resolvable at the scale of single beds, although replacement series through shallow-to-deepening cycles may display some features that parallel true succession. Replacement in marine communities may be relatively chaotic, but, more commonly in offshore settings, it appears to involve lateral, facies-related shifting of broad biofacies belts, or habitat tracking. Tracking patterns may be nearly symmetrical in areas of low sediment input. However, replacement cycles are commonly asymmetrical. The asymmetries involve both apparent and real effects; deletion of portions of facies transitions at sequence boundaries or condensed sections leads to artificial asymmetries. Alternatively, in areas proximal to siliciclastic sources, tracking asymmetries arise from the markedly higher sedimentation rates during regressive (late highstand) than transgressive phases. Replacements may also involve immigration of species into a sedimentary basin, either as short-lived events (incursion epiboles) or as wholesale faunal immigrations. The latter will typically follow intervals of extinction/emigration of the indigenous faunas. Both large and small immigration events appear most commonly during highstands (transgressive peaks), which may be associated with altered water-mass properties, and may open migration pathways for nekton and planktonic larvae. At least in isolated basins, allopatric speciation may also occur during fragmentation of habitats associated with regressions.

Finally, there are predicted and empirical correlations between sequence-producing sea-level fluctuations and macroevolution. Major extinctions may be associated with habitat reduction during major regressions (lowstands), or with anoxic events during major transgressions. Generally, rising sea level may be correlated with evolutionary radiations. Hence, some ecological-evolutionary unit boundaries may correlate either with sequence boundaries or maximum flooding surfaces. However, in other cases, no correlation has been found between macroevolutionary patterns and sequence stratigraphy. The situation is obviously complex, but sequence stratigraphy at least provides a heuristic framework for developing and testing models of macroevolutionary process.

INTRODUCTION

One of the great challenges of the Earth sciences is the development of “bio-geo-history.” This is an integrated view of global change that encompasses the complex interplay of biological and physical processes over a hierarchy of time scales ranging from the geologically instantaneous to hundreds of millions of years. A potentially fruitful area of integration lies at the interface between paleoecology and evolutionary studies, on the one hand, and sequence stratigraphy in its relationship to global sea-level and climatic changes, on the other (Kauffman and Sageman, 1992; Sageman, 1992; Gómez and Fernandez-López, 1994).

The principles of sequence stratigraphy, originally based on seismic studies of continental shelf strata and formulated by Vail et al. (1977a, b) and Mitchum et al. (1977), have subsequently been refined and applied to a broad array of marine and non-marine depositional systems (Wilgus et al., 1988; Van Wagoner et al., 1988; Vail et al., 1991; Emery and Meyers, 1996). Sequences are of variable duration, spanning hundreds of thousands to millions of years and have been subdivided by some authors into different scales: second-order supersequences, spanning tens of millions of years; third-order sequences with durations typically estimated at 1.5 to 5 million years; and fourth-order sequences, or subsequences, that span about 100 thousand to a million years. Regardless of scale, however, sequences share common patterns in terms of recorded fluctuations in water depth and sedimentation. Depositional sequences are internally conformable packages of strata bounded by marine to subaerial erosion surfaces (sequence boundaries) formed during sea-level lowstands. For most shallow marine settings, lowstand deposits are poorly developed. Typically, the sequence boundary also represents a transgressive surface at which shallow marine deposits of a transgressive systems tract unconformably overlie more offshore marine facies, the lowstand being represented only by the erosional unconformity itself (Baum and Vail, 1988; Posamentier and Vail, 1988; Mey-
ers and Milton, 1996). A second important surface, the maximum flooding surface or surface of maximum starvation, separates retrogradational (overall deepening upward) transgressive deposits from those of the overlying early highstand. Deepest water conditions are typically recorded in highly condensed strata immediately above the maximum flooding surface (Baum and Vail, 1988; Loutit et al., 1988; Meyers and Milton, 1996). The highstand display aggradational to progradational (shallowing upward) stacking patterns of small-scale subsymmetrical to shallowing upward cycles or parasequences. Thus, a typical depositional sequence displays a pattern of decreasing terrigenous sedimentation rates in the transgressive systems tracts, culminating in a condensed section and/or a surface of maximum sediment starvation; depending upon local conditions, intrabasinal carbonates may or may not accumulate in shallow marine environments during this time (Sarg, 1988; Emery, 1996). Siliciclastic sedimentation rates will increase in concert with shallowing in many prograding highstand systems tracts, resulting in coarsening upward successions (Posamentier et al., 1988; Posamentier and Vail, 1988; Meyers and Milton, 1996). However, in some cases, actual drop in sea level may cause forced regressions (Meyers and Milton, 1996); under these conditions, a minor erosional surface or condensed bed may separate early (aggradational) and later (progradational or regressive) portions of the highstand; Brett (1995) referred to this type of condensed bed as a “precursor bed.” Such beds are typically overlain by successions displaying marked shallowing upward trends.

A number of patterns of paleoecological and even evolutionary change appear to correlate with fluctuations in water depth and sedimentation through the course of depositional sequences. Sequence stratigraphy, therefore, may provide a key to the interpretation of these patterns, as well.

In recent years, paleontologists have begun to develop integrative models of depositional environments and paleoecology (Valentine, 1973; Einsele and Seilacher, 1982; Dodd and Stanton, 1990; Miller, 1990; Einsele et al., 1991) and evolutionary ecology (Valentine, 1985; Walliser, 1986a; Bayer and Seilacher, 1985; Donovan, 1989; Kauffman and Walliser, 1990; Ross and Allmon, 1990; Eldredge, 1990; Lees and Edwards, 1993; Erwin and Anstey, 1995). However, until recently, there has been little attempt to meld these approaches with the paradigms of sequence stratigraphy. Because paleoecological changes are closely correlated with fluctuations in sea level and sedimentation, one may predict many genetic relationships between fossil distributional patterns and depositional sequences.

The relationship between paleoecology and sequence stratigraphy is actually twofold. First, data from the fossil record may provide key information on depositional environments critical to the interpretation of marine sedimentary cycles and, thereby, to the recognition of ancient cycles and sequences. Second, the sequence stratigraphic framework provides a predictive model within which to explain various paleoecological phenomena: iterative cycles of ecophenotypic change, faunal or community-level tracking, and various perturbations in marine paleoecology that relate to changes in water depth, sedimentation, or other parameters that are tied to cycles of relative sea-level rise and fall.

Sequence stratigraphy provides a temporally constrained framework for the evaluation of ecological and evolutionary events. For example, it may permit precise evaluation of the timing of immigration, extinction, or origination of new taxa in a region or, with less precise resolution, on global scales. Unfortunately, the processes of sedimentation and erosion that produce sequence boundaries, condensed intervals, and flooding surfaces also impose an inherent bias on the fossil record that may produce artifacts in the apparent distribution of fossils. It is critical that paleontologists recognize and attempt to avoid these potential pitfalls in literal interpretation of the fossil record (Jablonski, 1985; Ross and Ross, 1988, 1994; Holland, 1995). Nonetheless, the same processes of sea-level, climate, and sediment-supply fluctuation that create depositional sequences also may have strong biological impacts. Immigration, origination, and extinction are commonly related to these factors, so that there may be important correlations between evolutionary patterns and sequence stratigraphy.

In a companion paper (Brett, 1995), I considered the relationships of sequence stratigraphy to biostratigraphic and taphonomic patterns. Herein I focus upon the dual relationship of sequence stratigraphy with paleoecology—the use of paleoecological data in recognizing and interpreting sequences, and the real and apparent effects of sequence-generating phenomena on patterns of fossil organism distribution and evolutionary paleoecology.

FOSSILS AS PALEOENVIRONMENTAL TOOLS IN SEQUENCE STRATIGRAPHY

Information derived from fossils in sedimentary sequences may be of critical importance in the interpretation of sequence patterns. This is particularly important for the inference of ancient water depths or paleobathymetry; however, evidence for changes in substrate consistency, sedimentation rate and turbidity changes, and bottom-water oxygenation may also provide insights into the environmental responses to sedimentary cycles and sequences. Taphonomic features related to sequence stratigraphy are discussed in Brett (1995); herein I focus on paleoecological approaches.

Water Depth

Paleontologic data frequently provide a far more sensitive gauge of relative water depth or even absolute depths than do sedimentologic features. Paleontologic data provide a number of potential constraints on relative and absolute water depths that may be extremely important in establishing the magnitude of sedimentary cycles (Benedict and Walker, 1978; Brett et al., 1983). Particularly valuable indicators include marine algae, especially dasychitaceans and certain types of endolithic green algae, and cyanobacteria. For example, Beadle and Johnson (1986) used cyclocrinoids to demonstrate that certain Silurian facies accumulated in shallow photic shelf conditions. Other lines of evidence for depth include evidence from orientation and implosion of ammonites, eyes in various arthropods, and hermatypic corals (Brett et al., 1993).
Oxygen isotopic data derived from calcitic shells also may be related to depth variations in some cases. For instance, Adlis et al. (1988) observed cyclic variations in δ¹⁸O values in non-luminescent (unaltered) brachiopod shells through Pennsylvanian cyclothems. Shells with highest values (coolest temperatures) occurred in highstand facies (deepest and coolest water). Conversely, Railsback et al. (1990) used a combination of oxygen isotopes and punctal density in Middle Ordovician brachiopods to infer the presence of warm, saline bottom waters in the Taconic foreland basin.

The relationships between ichnofacies and paleobathymetry, established by the seminal research of Seilacher (1967), have been supported in a general sense by numerous case studies (Fig. 1B–E; see revisions and updates of Frey et al., 1990; Maples and West, 1992, and articles therein; Droser and Bottjer, 1993; Bottjer and Droser, 1994; Goldring, 1995). However, factors other than water depth (e.g., substrate consistency and oxygenation) exert a very significant influence on the distribution of trace fossils, leading Frey et al. (1990) to conclude that only weak and indirect relationships exist between trace fossils and depth. Moreover, certain trace makers may have shifted their environmental positions, primarily in an onshore to offshore direction through the Phanerozoic (see Droser and Bottjer, 1993; Bottjer and Droser, 1994). Nonetheless, for a given time interval and substrate type, ichnofacies may still provide useful clues to relative water depth. Thus, vertical dwelling burrows of the Skolithos ichnofacies typify nearshore sands, especially in the early Paleozoic. Conversely, grazing traces (Nereites ichnofacies) characterize oligotrophic deep water muds, at least in the Mesozoic-Cenozoic.

A further application of paleontologic data to interpretation of paleobathymetry makes use of the predictable recurrence of particular benthic biofacies with depth zones. This approach, pioneered by Ziegler (1965), has proven exceptionally useful. Many biofacies do appear to be consistently arrayed with respect to depth (Ziegler et al., 1968; McKerrow, 1979; Boucot, 1975, 1982; Boucot and Lawson, 1998, and references therein). Furthermore, organisms tend to be evolutionary conservatively with respect to their preferred depth ranges. Hence, most genera and families seem to have occupied similar bathymetric zones for millions of years (Boucot, 1990c; Aberhan, 1994). Similarly, Holland (1997) observes that most Upper Ordovician brachiopod and bivalve genera display environmental stasis, although he also documents a few brachiopod species that appear to shift their habitat preferences through time. The generality of environmental stasis permits recognition of analogous depth positions in various systems even though these are populated by suites of distinct species. Fluctuations of fossil communities have been used extensively in recognizing ancient sea-level fluctuation, particularly in the middle Paleozoic (e.g., Johnson, 1987; Johnson et al., 1985). Cisne and Rabe (1978) and Cisne et al. (1984) outlined a detailed quantitative application of depth-related fossil associations referred to as gradient analysis. Application of these techniques may permit recognition of subtle cyclicity even in “basinal” mudrocks where sedimentological cues are lacking.

Salinity

Many organisms are sensitive to slight fluctuations of salinity. The presence of stenohaline organisms, such as echinoderms, articulate brachiopods, or cephalopods, may be a critical indicator of open marine conditions within particular portions of depositional sequences; they should typify later transgressive and early highstand deposits. Conversely, environments of reduced and/or variable salinity may be identified by the occurrence of low-diversity euryhaline faunas (e.g., lingulids, oysters; see Fürsich, 1994; Aberhan, 1994). Because such faunas characterize brackish-estuarine environments, they may be important in recognizing paralic, lowstand deposits. Moreover, in some instances, the appearance of marine ichnofossils at certain horizons of otherwise non-marine sediments may indicate minor marine incursions, associated with maximum flooding events (see Fig. 1C).

Substrate Consistency

The nature of sedimentary substrates typically varies in a predictable manner through sequences and parasequences. In particular, during times of relative low sediment input (e.g., in condensed sections), sediments may become relatively firm to cemented. Submarine erosion, commonly associated with lowstand intervals, may also remove superficial water-rich sediment, thereby exposing firm, ov ercompacted sediment to colonization by endofauna (Fig. 1D). Winnowing processes in shallow water occurring during later parts of the highstand may produce shell or other gravel deposits, which develop a firm armor or pavement on the sea floor capable of supporting a number of species that are restricted in habitat to colonization of hard substrates (Figs. 1A, E). These organisms, in turn, may contribute further skeletal debris, leading to positive taphonomic feedback (Fürsich, 1978; Kidwell and Jablonski, 1983; Miller et al., 1988; Kidwell, 1991). Finally, reduction of sediment input following periods of winnowing and shell-gravel accumulation may result in the formation of submarine hardgrounds at flooding surfaces.

Consistencies of certain substrates (e.g., hardgrounds) may be quite obvious; however, others cannot be so readily recognized (Fig. 1A, E). For example, how may we distinguish between a firm, overcompacted mud versus sediment that was, at the time of final burial, soft and plastic? Fossils, especially trace fossils, may provide very important clues in this regard and may be very useful in identifying key discontinuities within sequences (Figs. 1B–D). For example, Sellwood (1970), Savrda (1991) and Jones and Pemberton (1989), examined patterns of distribution of ichnofabrics in sedimentary sequences. Sequence-boundary unconformities and surfaces of maximum starvation display distinctive omission trace fossil suites (Figs. 1, 2). Where the latter are developed as firm- or hardgrounds, sharply defined burrows or borings of hard substrate-penetrating organisms are common (Fig. 1B,D,E). Deep, well-defined burrows, including Thalassinoides and Spongeliomorpha, are particularly well developed at ravinement (transgressive) surfaces where overconsolidated substrates have been exposed by submarine erosion (Kidwell and Aigner, 1985; Bayer, Allheimer, and Deuchle, 1985; Landing and Brett, 1987; Savrda, 1991; Taylor and...
Figure 1—Body and trace fossils as indicators of paleoenvironment and of significant stratal surfaces. (A) Biogenic indicators of substrates of varying consistency from soft (on left) to firm, and hard (right). (a) Nuculid bivalve, shallow infaunal deposit feeder. (b) Soft-substrate trace fossil Chondrites. (c) Pellet-lined burrow Ophiomorpha. (d) Burring heart urchin. (e) Infaunal suspension-feeding bivalve. (f) Sharply-defined dwelling burrow Thalassinoides. (g) Trace Spongeomorpha. (h) Mechanical mud-boring bivalve Petricola. (i) Chemical rock-boring bivalve Lithophaga. (j, k) Crinoid holdfast and oyster cemented to hardground surface. (l) Trypanites (borings). (m) Serpulid worm tubes and bryozoans encrusting on cemented wall of relict burrow. (B–E) Ichnological signatures of stratigraphically important surfaces. (B) Marine flooding surface. (C) Minor marine incursion into non-marine environment. (D) Omission surface associated with shallowing and overtarn by condensed bed (i.e., precursor bed; see text). (E) Omission surface recording interval of sediment starvation and relict development in offshore facies (e.g., surface of maximum starvation associated with early highstand). Adapted from Goldring (1995), after Taylor and Gawthorpe (1993).

Sedimentation Rate and Turbidity

Relative rates of sedimentation and associated levels of water turbidity may be expected to vary predictably within a sedimentary sequence. However, the assessment of
these rates is exceptionally difficult. It is closely tied to the issue of time resolution in rocks, which has been addressed recently by Kidwell and Behrensmeyer (1993, and papers therein). In addition to the taphonomic and trace fossil indicators suggested above, paleoecology may provide an important tool in this endeavor.

Assemblages dominated by suspension feeding, endo- and epibenthic organisms tend to be well-developed under conditions of low sedimentation rates, low turbidity, and firm substrates (Rhoads et al., 1972; Scott, 1978; Fürsch, 1978; Elder, 1987). Hence, a ratio of deposit to suspension feeders may be a useful predictor of relative sedimentation rates in sedimentary sequences.

If there is independent evidence for normal oxygenation, variations in sedimentation rates may be inferred from the relative concentration of trace fossils in vertical successions (e.g., Savrda and Bottjer, 1994). Thus, Mortimore and Pomerol (1991), Taylor and Gawthorpe (1993, see Fig. 1B–E), and Savrda and Bottjer (1994) have documented the significance of concentrated, cross-cutting trace fossils in recognizing minor omission and scour surfaces, including marine flooding surfaces (Figs. 1, 2). In contrast, the occurrence of numerous discrete burrows may indicate a higher sedimentation rate. Furthermore, certain trace fossils, such as Zoophycos, appear to be sensitive indicators of increased sedimentation rates (Brett, 1995). Storm-event beds may also be recognizable from distinctive suites of “opportunistic” trace fossils (Vossler and Pemberton, 1988; Pemberton and MacEachern, 1997). Such types of trace fossil occurrences should occur predictably during middle-to-late highstands of depositional sequences that are characterized by shallowing and increased sedimentation rates. In dysoxic facies it may be difficult to distinguish the effects of sedimentation from variable bottom-water oxygenation (see below), although recognition of oxygen-related ichnofossils and trace fossil tiering aid in this regard (see Savrda and Bottjer, 1994).

Truncation of trace fossils, such as borings with distinctive profile shapes (e.g., Warme, 1975; Taylor and Gawthorpe, 1993; Fig. 1D), may provide evidence for erosion of the substrate. Such truncation may occur at hardgrounds and other discontinuity surfaces. Goldring (1971) used alternations of protrusive and retrusive spreiten in the trace fossil Diplocraterion yoyo to infer fluctuating depositional/erosional conditions (Fig. 1C). In a related line of reasoning, Wetzel and Aigner (1986) used tiered (i.e., depth partitioned) suites of trace fossils as a “yardstick” for seafloor erosion. Because particular types of traces occupy approximately consistent depths, it is possible to estimate the amounts of sediment removed when only deeper tiers are preserved below truncation surfaces. Such tools may be useful in identifying submarine erosion surfaces associated with sequence or parasequence boundaries.

The abundance of light-sensitive or photosynthetic organisms may provide a good indicator of a low sedimentation rate and turbidity. Turbidity-sensitive taxa, such as corals and suspension-feeding echinoderms, whose water vascular systems may be clogged by excess fine-grained sediments (Rosenkranz, 1971; Selikacher, Reif, and Westphal, 1985), may also be useful indicators of low rates of sedimentation and slight water turbidity.

The distribution of these organisms is expected to vary consistently within a sedimentary sequence. For example, higher-diversity assemblages of suspension-feeding organisms will typically occur during transgressive phases, when turbidity and sedimentation were relatively low as a result of nearshore sediment entrapment. Conversely, the emptying of coastal sediment traps associated with sea-level drop should greatly increase the influx of fine- to medium-grained sediments into offshore areas (see Posamentier et al., 1988; Posamentier and Vail, 1988; Meyers and Milton, 1996). This will result in consequent negative effects on organisms that were intolerant of turbidity, and positive effects on primarily deposit-feeding forms that required increased amounts of organic detritus and/or soft substrate for their survival.

### Bottom-Water Oxygenation

While not directly related to the processes generating sedimentary sequences, the level of bottom-water oxygenation is highly sensitive to relative rise and fall of sea level. In particular, episodes of widespread anoxia or the development of large masses of low-oxygen bottom water are typically associated with transgressions (see Kauffman, 1981; Hallam, 1992; Wignall, 1994). Wignall has reviewed biotic evidence for low oxygen or dysoxic conditions near the substrate. While he finds no particular group of organisms to be diagnostic of this zone throughout geologic time, he does suggest a number of indicators, including overall diversity and the presence or absence of burrowing organisms, from which to interpret relative oxygenation. Batt (1993) used proportions of inferred pelagic to nektobenthic ammonoids as a proxy for paleo-oxygenation in Cretaceous cycles from the Western Interior basin.

A relatively sensitive tool for recognition of oxygenation events and cycles within offshore marine mudrocks was presented by Savrda and Bottjer (1991, 1994). Horizons of extensive piping of burrowed, organic-free sediment into black, laminated muds indicate periods of benthic oxygenation. Likewise, a decrease in the diversity and depth of trace fossils may point to decreasing oxygen levels or de-oxygenation events. A tiered trace fossil model is generally applicable for recognizing relative bottom-water oxygenation on the basis of type and depth of burrows (Kauffman, 1981; Savrda and Bottjer, 1989, 1991, 1994; Sageman et al., 1991). Many deepening events (e.g., marine flooding surfaces in basinal sediments) are associated with the rise of the anoxic boundary and, as such, may be recorded as de-oxygenation events.

### Biotic Responses to Sedimentary Cycles and Sequences

Sedimentary sequences are the record of fluctuations in relative sea level, sedimentation, and other related environmental parameters. Hence, one may predict that an array of biotic changes will be reflected in their fossil assemblages. On the other hand, the preserved patterns of biotic change may be strongly influenced by changing preservation potentials. For example, certain portions of a spectrum of community replacement may be absent due to a lack of sedimentation or removal by erosion. Therefore, distortion of the original pattern of biotic fluctuation will be predictably severe at sequence boundaries and maximum flooding surfaces (condensed sections) of deposition-
al sequences (Holland, 1993, 1995; Ross and Ross, 1994). This bias may have the effect of producing apparently abrupt and simultaneous extinctions and biotic changes, even if original patterns were gradual and staggered; or, biases may sharpen truly abrupt turnover events (Holland, 1995). Conversely, lateral shifting of facies within depositional sequences may lead to a pattern of gradual first appearances of species (e.g., during immigration events) as a result of our inability to test for the presence/absence of facies-controlled species in local sections in which inappropriate facies are preserved. This is an expression of the smearing phenomenon originally documented by Signor and Lipps (1982).

We must carefully distinguish these artifacts of preservation from real biotic responses to transgressive-regressive cycles (see Jablonski, 1980, 1986). Probably the best approach to this problem is the application of a “time-environment” approach; specifically, the regional study of facies spectra in carefully correlated stratigraphic intervals, as advocated by Holland (1995, 1997). Clearly, such an approach is critical for a better assessment of the true timing of biological events; studies of fossil-distribution patterns in single sections or suites of locally restricted outcrops are plagued with stratigraphic biases and cannot discern a complete history of the original patterns. Sequence stratigraphy provides a framework for constraining time relationships of strata across facies changes. Ideally, it is possible to trace laterally displaced biofacies with regional study of the “time-slices” provided by single parasequences, systems tracts, or sequences (e.g., Elder et al., 1994; Fig. 3). This will provide a more complete picture of the actual first and last appearances of fossil species, and changes in the composition of biofacies. Also, it may be possible to trace sequence-bounding unconformities and condensation surfaces into areas of conformable and expanded sections; this procedure will help to fill in the missing pieces of regional biofacies history.

Holland (1995) has also proposed a method in which the apparent effects of hiatuses on species-range patterns may be assessed. In this approach, the patterns of biotic change, assuming gradual or constant species turnover, may be simulated for unconformable gaps of different magnitudes and those patterns compared with those of the actual fossil record. Observed abrupt shifts that exceed those produced as the artifact of truncated ranges may thereby be recognized as partially real biotic effects.

Assuming that spurious effects can be recognized and accounted for, we may begin to interpret the ways in which ancient organisms responded to the environmental fluctuations that produced depositional sequences. The responses may be either ecological or evolutionary. Ecological (facies-related) explanations must be carefully considered and ruled out before the observed biotic changes are interpreted as evolutionary. As Jablonski (1980) succinctly pointed out, patterns of changing diversity, endemism, eurytopy, and other features typically recorded during transgressive-regressive cycles may best be explained in terms of migration of fixed onshore-offshore ecological gradients. Hence, habitat tracking (see below), rather than evolutionary responses to the “stresses” associated with shifting sea level, may account for a majority of cases of faunal change in local sedimentary sequences. This phenomenon of faunal migration was already discerned and cogently analyzed long ago by Williams (1903, 1913).

Ecological (non-evolutionary) responses to sequence or parasequence-producing environmental fluctuations include community replacement, ecophenotypic changes, minor species-level substitutions and fluctuations (episodes), and immigration/emigration of species into/from the local ecosystem. These responses will be considered in the next section. Evolutionary changes, including extinction, species evolution and evolutionary radiation, in response to sequence-producing environmental fluctuations, will be dealt with in the last section of this paper.

COMMUNITY REPLACEMENT

Whole changes in species composition are recorded in many sedimentary cycles. Such community replacement commonly involves a predictable, facies-related recurrence of species. Where the latter can be related to lateral shifting of biofacies it is termed habitat tracking (Figs. 3–6). Before further discussion of replacement and tracking, it is necessary to carefully distinguish these phenomena from another pattern that has often been incorrectly conflated with replacement: succession.

Replacement vs. Community Succession

In the past, some paleontologists have used the term succession to denote long-term changes in community structure within local sections. Neontologists have generally defined succession as short-term (tens of years) sequential change in community structure, generally in response to environmental changes induced by the organisms themselves (Odum, 1971; Connell and Slaytor, 1977; Levinton, 1982). As a result of time-averaging, it is unlikely that such short-term succession can be resolved in most strata (Schindel, 1980, 1982; Sadler, 1981), although Walker and Alberstadt (1975) illustrate possible true cases in level-bottom epibenthic communities and fossil reefs. In any case, such examples lie at the lower end of resolution for the fossil record, typically at the scale of individual rapidly buried bedding planes. Such short-term “autogenic” succession is clearly of a different temporal magnitude than the faunal replacements, which typically are observed through several meters of strata in sequences or parasequences, and must span thousands of years (Bretsky and Bretsky, 1975; Walker and Alberstadt, 1975). Rollins et al. (1979) tried to distinguish between replacement and succession in a Pennsylvanian cyclothem. However, their example of succession still represented a significant gradational change in assemblage composition, spanning a major portion of a cycle. Hence, it is best interpreted as a shifting faunal gradient; i.e., gradual replacement, not succession.

Use of the term succession for the longer-term processes has caused considerable confusion; this term should be restricted to those rare cases in which changes in ecological time can be documented in the fossil record. Nonetheless, there may be an indirect relationship between short-term succession and longer-term replacement, as suggested by the work of Bretsky and Bretsky (1975; see Fig. 3 herein). For example, early successional stages in marine communities are typified by low-diversity assemblages of gener-
FIGURE 3—Pattern of asymmetrical faunal replacement (tracking) within probable sedimentary cycles of the Upper Ordovician Nicolet River Formation of Quebec. Vertical columns represent an ordered series of distinctive species associations with diversity generally increasing from 1 to 4 but declining slightly in 5 and 6. These associations were termed “successional stages” by Bretsky and Bretsky (1975), but represent relatively long-term changes herein interpreted as different depth-related community types (or biofacies). Original diagram has been modified from Bretsky and Bretsky (1975) to reflect reinterpretation of “successional series” as community replacements in about 17 small-scale depositional sequences, labelled S-1 to S-17. Alternate sequences are shaded to highlight sequence boundaries (SB). Inferred maximum flooding surfaces (MFS) are denoted by dotted lines. Typical asymmetrical pattern of community replacement (left to right shift in types 1–6) during inferred main, shallowing-upward highstand portions of cycles are best exemplified in S-2, S-5, and S-6: Abrupt shifts back from community types 5 or 6 to type 1 are inferred to represent sediment-starved discontinuities at flooding surfaces: Minor intervals of right to left shifting of biofacies (e.g., base of S-7) are inferred to represent transgressive systems tracts. Community types (biofacies) 3, 4, and 5A appear to be absent in cycles above S-7. Coarse intervals occur at 400–500', 625–1050', and 2100–2300'.

alized eurytopic species (Johnson, 1972; Walker and Alberstadt, 1975; Bretsky and Bretsky, 1975); as such, this sere will be similar in many areas. If communities are down-graded to pioneer series by storm-generated disturbance of the seafloor (as in the model of Johnson, 1972), then the average state of paleocommunities may be determined by the frequency of that disturbance. Thus, near-shore assemblages may be dominated by “pioneer”-type communities, as these areas are frequently disturbed. Polikloaerobic settings, characterized by frequent fluctuation of an oxic/anoxic boundary, may display similar patterns (Wignall, 1994). In contrast, less disturbed, offshore, and fully aerobic biofacies will more commonly have an opportunity to progress to more complex stages of coloniza-
tion (e.g., hard substrate encrusters settling on skeletons of “pioneer colonizers,” Walker and Alberstadt, 1975; Kidwell and Jablonski, 1983).

The time-averaged remains of these stable communities will, on average, appear to be in more “mature” successional stages. Nonetheless, because they are effectively random, major disturbances will still preserve earlier successional stages occasionally (i.e., when two major storm events happen to be closely spaced in time), and these will resemble “nearshore biofacies.” True successional series, worked out from such fortuitous samples in offshore areas, will resemble the general pattern of time-averaged fossil assemblages in an onshore-offshore gradient. Lateral faunal tracking through transgressive sections might then
preserve a long-term pattern of facies replacement that somewhat mirrors true succession, as in Bretsky and Bretsky's (1975) example.

Non-Tracking Species Replacements

A common perception, especially among neontologists and paleobiologists working in the Pleistocene, is that environments are in a constant state of flux (see Bennett, 1990; DiMichele, 1994). Consequently, species associations occupying a given area are also very ephemeral. Although broadly-defined biofacies may display some gross similarities through time, local associations or communities are constantly reforming with new casts of characters being assembled from pools of largely independent and rather eurytopic species. Such chaotic changes in species assemblages, or non-tracking replacements, should lead to a rather unpredictable mosaic pattern of faunal distribution in the fossil record. A few authors have documented patterns that might be interpreted in this way. For example, Miller (1986) and Miller and Dubar (1988) infer that some Neogene fossil molluscan communities represent ephemeral groupings assembled from various species pools following disturbances. Mosaic patterns of this type may occur where habitats are highly patchy and/or subject to frequent disturbances (Johnson, 1972), as in very nearshore environments. However, even in such settings, time-averaging may tend to smooth out the local patchiness, leading to more predictable facies-related distributions.

A type of non-tracking replacement (“long-term community succession”) was postulated to have taken place in “unchanging” environments represented in the Lower Devonian of Oklahoma (Walker and Alberstadt, 1975). The authors cite the occurrence of generally uniform carbonate mudrock lithofacies as evidence for absence of environmental change. However, this seems improbable given the thickness of the unit (>30 m) and the extent of the faunal change. Not all mudrock represents the same environment, and this situation is probably best interpreted as faunal replacement in response to subtle environmental changes.

Habitat Tracking

Biofacies may occupy very broad, monotonous belts elongate parallel to shore in open shelf and epicontinental environments. Migration of such belts in response to sea-level fluctuations may yield a very predictable pattern of replacement through sedimentary cycles that behaves in accordance with Walther’s principle of facies (Anderson, 1971; Figure 4 herein). The repeated documentation of predictable, recurrent associations of species that closely parallel sedimentary cycles (Ziegler, 1965; Anderson, 1971; McKeirrow, 1979; Cisne and Rabe, 1978) suggests that a pattern of high-fidelity habitat tracking is typical of many marine benthic communities. Provided that environmental changes are not too pervasive or rapid, most species associations appear to migrate or track their favored environment. Habitat tracking is fairly localized (perhaps tens to a few hundreds of kilometers of migration perpendicular to shoreline over tens to 400 Ka) for smaller scale sea-level oscillations recorded by parasequences or minor sequences (Elder et al., 1994). In major sea-level fluctuations, recorded by sequences, the geographic displacement may amount to hundreds of kilometers, and faunal recurrence within a particular region may be on the order of hundreds of thousands or even a few million years. Thus, in the middle Paleozoic of the Appalachian Basin, certain (shallowest or deepest water) biofacies may only appear once in each third-order sequence, and yet return with considerable fidelity. An example of this is provided by recurrence of coral beds in the Middle Devonian Hamilton Group, where the shallowest water facies are associated with transgressive systems tracts of each of seven sequences. In all of these cases, however, the biofacies appear to have continuously occupied particular mi-
grading environments; that is, the faunal gradients were more or less static throughout the interval. However, another form of very long-term recurrence apparently takes place by reintroduction of suites of species after their elimination from an entire region, and the development of entirely different biofacies gradients. This form of tracking, originally recognized by H.S. Williams (1903, 1913) in the Devonian of the Appalachian Basin, is a distinct phenomenon reflecting emigration and immigration of entire faunas (see below). Patterns of complete, species-by-species tracking, in which communities recur with absolute similarity, are rarely observed. Just as Walther’s “law” is a valid and highly useful generality with many exceptions in detail, so too the notion of faunal tracking should be viewed as a reasonable first approximation to the actual process. In actuality, no two sedimentary cycles have developed under exactly the same conditions, so it is not surprising that biofacies in distinct sedimentary cycles or even different phases of the same cycle may differ in details of species composition, dominance, or rank position, etc. (Bennington, 1994; Bambach and Bennington, 1996).

What is surprising is that biofacies may maintain very similar compositions, species richness, rank ordering, etc., for intervals of time up to several million years.

**Symmetrical Tracking**

Within a single stratigraphic section, habitat tracking may produce a predictable vertical stacking pattern of biofacies that appear in a nearly symmetrical cycle (Figs. 3–5). Such “symmetrical tracking” patterns represent simple lateral shifting of bathymetrically-zoned biofacies, perpendicular to facies strike (shoreline), in response to relative rise or fall of sea level. This simple Waltherian pattern is assumed in models of “coenocorrelation” that make use of fluctuations in fossil “communities” or species associations to determine relative sea-level curves (e.g., Ziegler, 1965; Anderson, 1971; Cisne and Rabe, 1978; Cisne et al., 1984; Johnson et al., 1985).

In offshore areas where the rate of siliciclastic sedimentation remains fairly low throughout a sedimentary cycle, a nearly symmetrical pattern of faunal tracking may be observed (Figs. 4, 5). For example, many carbonate and mixed siliciclastic-carbonate successions of the Ordovician to Devonian in the Appalachian basin display a predictable spectrum of litho- and biofacies changes (Cisne and Rabe, 1978; Brett et al., 1990). Figure 5 shows a typical cycle in the Middle Devonian Hamilton Group of western New York State (see Savarese et al., 1986), a depth-related gradient of change from (a) black laminated shales with sparse, low-diversity, dyssoxic faunas, through (b) gray mudstone facies with moderate-diversity assemblages of small brachiopods, nuculid and other small mollusks, that proceeds upward to (c) highly calcareous mudrocks and limestones with high-diversity assemblages of corals, brachiopods, bryozoans, and pelmatozoans. A “mirror-image” spectrum of biotas occurs in the upper or transgressive half cycle, which is typically about as thick as the shallowing portion of the cycle. Hence, species associations appear to shift back and forth in a cyclic pattern that mimics the sedimentary cycles.

Basinal areas may display similarly symmetrical, but more subtle, patterns of faunal change. Such sections are typically somewhat expanded as a result of entrapment of sediments near depocenters. These sections display a smaller range of facies change than do those representing shallower water areas. In both transgressive and highstand (including regressive) phases, organisms sensitive to higher rates of sedimentation or turbidity, such as corals, may be rare or absent.

Although there are minor differences in relative frequency of the most common taxa and perhaps in the appearance or absence of a few rare taxa, the assemblages on either side of these symmetrical cycles appear remarkably similar. Furthermore, detailed lateral correlation indicates that these assemblages do in fact persist and migrate in a Waltherian manner during rise and fall of sea level. However, in areas in which erosion or siliciclastic input are major factors, the sedimentary cycles and the fossil communities within them may appear more markedly asymmetrical (Figs. 3, 4, 6).

**Asymmetrical Patterns: Artifacts of Preservation**

A good deal of the biofacies asymmetry observed in some sedimentary cycles may be attributed to incomplete preservation of intermediate facies. In the epicratonic seas, where subsidence rates were low, transgressive to early highstand systems tracts are best represented, while late highstand (regressive) facies are largely missing (Einsele, 1985; see Figs. 3 and 4 herein). The shallowest water facies, comprised of shell-rich or crinoidal transgressive limestones, are abruptly juxtaposed onto early highstand facies preserving a deeper-water faunal assemblage (Bayer, Altheimer, and Deutschle, 1985; Brett and Baird, 1996; see Fig. 4 herein). Erosion surfaces at the bases of the limestones are marked by a distinctive omission suite of trace fossils with well-preserved scratch marks indicating their production within overcompacted muds exposed by removal of considerable overburden (Kidwell and Aigner, 1985; Bayer, Altheimer, and Deutschle, 1985; Seilacher, Reif, and Westphal, 1985; Landing and Brett, 1987). Transitional, shallowing biofacies of the late highstand in the underlying sequence are absent because they have been removed by erosion associated with a lowstand maximum at the sequence boundary (Fig. 4). However, there are hints that the actual pattern of faunal tracking was nearly symmetrical. Where remnants of the truncated shallowing-upward succession are preserved below a sequence-bounding erosional surface, they appear very nearly identical to the analogous facies of the more completely preserved transgressive systems tract.

Elsewhere, particularly in siliciclastic-dominated shallow-water successions, portions of a tracking biotic spectrum may be lost at the surface of maximum starvation, through extreme condensation or even submarine erosion (Figs. 3, 4). This again imposes apparent asymmetries on the pattern of vertical faunal replacement. A good illustration of this is found in Breisky and Breisky’s (1975) detailed study of Late Ordovician faunas in the Nicolet River Valley of Quebec. Figure 3 shows several “successional cycles” (cycles of faunal replacement) that appear markedly asymmetrical due to the absence of intermediate stages (or biofacies). These patterns can be interpreted as progressions of community replacement through several shallowing-upward cycles or parasequences. The absence
FIGURE 5—Symmetrical community replacement (tracking) patterns in Middle Devonian biofacies. Representative cycle in distal, relatively sediment starved position, based on Centerfield Limestone of western New York State. Note nearly mirror image ordering of biofacies through a shallowing-deepening cycle (late highstand portion of one depositional sequence and transgressive systems tract of overlying sequence). Block diagrams illustrate biofacies or fossil associations plus typical bed stratigraphy. (a) Dysoxic, low diversity leiorhynchid brachiopod and cephalopod association in dark gray to black, laminated shale; (richness, \( R = 5 \text{–} 10 \) species); (b,f) Moderate diversity (\( R = 20 \text{–} 30 \) species) Ambocoelia association, in medium gray mudstone, dominated by small brachiopods and molluscs; (c, e) Diverse brachiopod and small rugose
of mirror-image deepening series probably reflects sedimentary condensation at the flooding surfaces of each sequence. Again, the asymmetrical pattern may be more apparent than real (Holland, 1995).

Asymmetrical Patterns: Biotic Causes

True biotic asymmetries in tracking result from the expected variation of sedimentation rate throughout a depositional sequence. Complex, along-strike shifting of biofacies may record the interplay of bathymetric and sedimentologic/substrate factors that control organism distribution. Specifically, where sedimentation rates vary markedly in shallowing (regressive) versus transgressive phases of a cycle, producing asymmetrical parasequences or sequences, faunal tracking patterns are complex and asymmetrical (Rollins et al., 1979; Holterhoff, 1992).

For example, in depositional environments proximal to sediment sources, cycles may be manifested as distinctly upward-shallowing progradational packages that commence with dark silty shales and pass upward through relatively thick successions of bioturbated silty mudstone, siltstone, and sandstones (Figs. 4, 6). In these areas, the succession of fossil assemblages of the late highstand (regressive) systems tract is quite distinct from that found in the coeval thinner sections more distal to the siliciclastic source area. Moreover, the pattern of faunal replacement in the late highstand (regressive) facies is distinctly asymmetrical with respect to that in the transgressive systems tract. Epifaunal and infaunal deposit-feeding organisms and their traces tend to dominate the regressive sediments. This presumably results from the greater availability of particulate food within the finer-grained portions of the siliciclastic sediment, as well as a higher degree of substrate instability (Fürsich, 1978; Scott, 1978; Elder, 1987). Bivalves, and quasi-infaunal brachiopods, as well as gastropods and certain trilobites, may occur abundantly in these mudrocks (Fig. 6).

The shallowest portions of siliciclastic-dominated sequences commonly display hummocky cross stratification, ripple marks, and other sedimentary structures that attest to physical processing of the sediments by storm waves and currents (Fig. 6). Correspondingly, less intense bioturbation is characteristic of these portions of these cycles. Vertical traces, such as Skolithos, may be predominant in certain layers, reflecting minor cutoffs in sedimentation. Coquinites of low-diversity, thick-shelled epibenthonic invertebrates, reemerge in certain layers, reflecting minor cutoffs in sedimentation.

The biofacies of the transgressive portion of the cycle typically resemble those in the symmetrical sediment-starved cycles distal to terrigenous source areas (Fig. 4; compare Figs. 5 and 6). They may include a wide array of epifaunal species that are absent or exceedingly rare in the regressive half cycle. The matrix of these beds is typically a fine-grained, slightly calcareous mudstone, although thin skeletal-hash beds or even semi-continuous fossiliferous limestones may occur in the basal transgressive systems tracts of these cycles.

These faunal asymmetries clearly reflect a distinct inequality of sediment supply in the regressive, as opposed to transgressive, phase of the cycle (Fig. 4). Sedimentation rates are higher and tend to increase during the late highstand as siliciclastic wedges prograde offshore, either in response to, or as a cause of shallowing. Conversely, siliciclastic sedimentation rates are lower and tend to decrease during transgressions. Only fine-grained, suspended siliciclastics are transported any distance offshore. Thus, the transgressive half cycle appears sedimentologically and faunally far more consistent over a broad area than does the regressive half. Organisms that are sensitive to or excluded by high rates of sedimentation may appear even in areas relatively proximal to the terrigenous source regions during this time. The fact that two distinct types of biofacies may occupy comparable bathymetric zones, and yet each recur with considerable fidelity, suggests that these biofacies are displaced laterally (along strike), tracking variations in sedimentation as well as depth (Fig. 4).

ECOPHENOTYPIC CHANGE THROUGH SEDIMENTARY CYCLES

Certain broadly adapted, eurytopic organisms may remain in a particular geographic area but display some morphological modification in response to local environmental change. Typically, this “modification” involves a non-evolutionary, ecophenotypic response. In actuality, this may involve a non-tracking response to environmental change, or ecomorphs of a species may themselves be tracking environments.

A number of studies have sought to relate repetitive cycles of morphological change to cycles of sedimentary environmental change. Such studies are not without difficulties, however. Kidwell and Aigner (1985) discuss the problems of discriminating ecophenotypic variation in condensed sections, wherein mixing of remains of several generations of organisms and, in some cases, those representing different environments may occur within the same bed. Interpretation of ecophenotypic change, as opposed to microevolution, may also be ambiguous. Kelly (1983) documented increasing mean values of some five of eight variables in the bivalve Lucina anodonta from deepening-upward successions in Miocene shell beds from Maryland. Kelly suggested that the progressive change represented a case of micro-evolution in an otherwise generally stable assemblage of fossils. However, as a similar pattern repeats through three cycles, represented by major shell beds, Kidwell and Aigner (1985) concluded that it
FIGURE 6—Asymmetrical community replacement (tracking) in proximal correlative of same cycle illustrated in Figure 4 (based on Chenango Siltstone Member in central New York State). Note that biofacies in middle regressive facies are dominated by low-diversity brachiopod and mollusc faunas with abundant Zooxysu. Also, biofacies of analogous depths in transgressive phase are distinctly more diverse and closely resemble those of the more distal sediment starved cycle shown in Figure 5. Fossil associations include: (a) Small brachiopod-dominated, moderate diversity ($R = 20–30$ species) Ambocoelida association with local thickets of auloporid corals found in precursor bed; (b) lower diversity ($R = 10–20$ species) small brachiopod and mollusc-dominated association in silty mudstone; (c) patchy, moderate diversity ($R = 30–50$ species)
is more likely to represent a case of ecophenotypic change that was reversible and repetitive through sedimentary cycles.

A particularly fruitful line of investigation is the morphological response of sedentary organisms to changes in substrate that vary predictably in small-scale cycles or parasequences. Seilacher, Matyja and Wierzbowski (1985) and Bayer, Johnson and Brennan (1985) observed parallel ecophenotypic gradients within Jurassic and Pleistocene oysters that neatly parallel small-scale shallowing-upward cycles (Fig. 7). Morphological trends, including flattening and broadening of the shells, in each case reflect the development of firm, sometimes shell-rich sediment with decreasing mud content as a result of an increased frequency of disturbance and winnowing events near the tops of the cycles (Bayer, Alteimer and Deutchle, 1985).

Similarly, Kidwell and Aigner (1985) discussed a case of variation and morphology of the Eocene clam *Carolina placunoides*, which apparently reflects alternation of colonization strategies. Hard substrate encrusting forms were broad and flat, while deeper, cup-shaped forms developed stacks of mutually supported shells on soft substrate. Alexander (1975) observed similar ecophenotypic variation in shells of Late Ordovician strophomenid brachiopods from Ohio. Broadening and flattening of shells was characteristic of offshore, muddy environments, while more strongly concavo-convex morphotypes typified firmer sediments of cycle caps.

In these cases, the skeletal morphology displays a consistent trend of change through a small-scale sedimentary cycle, which is readily related to the dynamics of sediment input and winnowing and the development of variable substrate consistencies. In other instances, repetitive ecophenological cycles may parallel sedimentary cycles without being so obviously related to functional constraints. Bayer (1970) and Bayer and McGhee (1985) report consistent ecophenological gradients in genera of Jurassic ammonites; smooth, evolute morphs typify offshore claystone facies near bases of cycles, whereas evolute, highly sculptured forms occur in oolitic limestones, and spheroïd forms with tricarinate keels characterize condensed limestones. While the causes of such morphological response remain ambiguous, especially in nektobenthic organisms, nonetheless, they may provide important links between organism paleoecology and changing sedimentary environments.

ECOLOGICAL EPIBOLES AND OUTAGES

Ecological change in response to changing environmental parameters may involve simple changes in relative dominance of species. For example, a normally rare species becomes common and/or widespread in a thin stratigraphic interval, forming an “ecological epibole.” Conversely, “outages” represent anomalous rarity or absence of a normally common species (Brett and Baird, 1997). Ecological epiboles represent genuinely biological phenomena in which conditions temporarily become conducive for colonization or proliferation of a species that is normally rare within the basin. The species may flourish over a wide area during these times. Particularly problematic is the fact that these epiboles also may involve cross-cutting relationships among facies. In outages, the opposite situation pertains; some factor in the environment inhibits or locally eliminates a species that ordinarily is common or even dominant.

Certain taxa may display multiple epiboles, each occurring in analogous phases of sedimentary cycles, albeit not in each successive cycle. This indicates that conditions conducive to proliferation of the species are associated with certain combinations of environments that do not re-
occur with every cycle. In mid-Paleozoic faunas, epiboles tend to occur particularly during the transgressive systems tracts of third- and fourth-order sequences. The regressive (late highstand) portions of cycles tend to be characterized by eurytopic faunas that recur very predictably in each cycle. In contrast, unusual environments associated with the development of variably sediment-starved conditions may permit temporary proliferation of stenotopic species that are generally rare. Ecological epiboles and outages presumably reflect slight differences within a generally persistent environment that favor or inhibit a few species while leaving the majority of the fauna unaffected. In most cases, the environmental perturbations responsible for epiboles or outages are not apparent from sedimentary facies. However, clues as to causative agents may be sought in isotopic or trace-element geochemistry.

**REPLACEMENT BY LARGE-SCALE IMMIGRATION**

Not all faunal replacements involve shifting or proliferation of indigenous species. If, and only if, replacement by ecological tracking of local faunal elements can be ruled out, it may be possible to discern patterns that are generated by immigrational and/or evolutionary processes in relation to depositional sequences.

In some instances, faunal change involves influx of “exotic” species (incursion epiboles of Brett and Baird, 1997) or wholesale incursion of an entire fauna from another basin or province. The latter will commonly occur in association with local extinction of many indigenous species. However, this is not necessarily true. For example, in the case of the Richmondian invasion, a number of invertebrate species were added to each of several biofacies in the Upper Ordovician of the Cincinnati arch region without loss of many indigenous taxa (Patzkowsky and Holland, 1996; Holland, 1997).

Episodic immigration events are particularly typical of nektonic forms, such as ammonoids, and benthic forms with planktonic larvae. Notable examples include widespread ammonoid incursions that are closely associated with marker beds in the Jurassic of Germany (see Bayer, Johnson and Brennan 1985; Figure 8). Such incursions may reflect unusual sedimentary conditions; thus, the development of widespread shell gravels in the Jurassic basin seem to have permitted the influx of hard substrate encrusting as well as certain nektobenthic ammonoids (Bayer and McGhee, 1985; Bayer, Johnson and Brennan, 1985). Similarly, Hagdorn (1982, 1985) demonstrated that widespread beds of brachiopods and crinoids typically occur at the caps of shallowing-up carbonate cycles within the Triassic Muschelkalk Limestone of Germany. Cementation of the substrate associated with marine flooding surfaces developed hardgrounds that permitted the extensive influx and colonization of species that required hard substrates for attachment. These species were normally restricted to shoal areas on the margins of the Tethys sea. Altered circulation and climatic pattern during sea-level highstands may promote major immigration episodes. For example, the abrupt appearance of a diverse fauna within a condensed concretionary limestone in the Upper Cretaceous Graneros Shale may be related to the influx of a warm subtropical water mass into the Western Interior Basin during a major eustatic sea-level rise (Kauffman, 1986). Normally isolated biogeographic provinces may also be connected during maximum flooding events, allowing the transfer of larvae between provinces (Eicher and Diner, 1985; Kauffman, 1986).

The existence of “recurrent” faunas separated by hundreds of meters of strata bearing completely dissimilar faunas indicates a long-term form of faunal migration, as noted around the turn of the century by Williams (1903, 1913). In his study of recurrent *Tropidoleptus* or Hamilton faunas, Williams observed that an entire suite of species may recur long after their apparent extinction in a region. This indicates a process similar to, but distinct from habitat tracking, in that the recurrent fauna or biofacies seems to have been replaced by another suite of tracking species in its appropriate sedimentary environments, as inferred from position in cycles and lithofacies. Such faunal recurrence may involve displacement and reintroduction of entire or partial biofacies from a region within the basin not generally represented by exposed strata, or another depositional basin or province. This faunal outage and recurrence is probably analogous to the phenomenon identified as species outages, except that it involves wholesale migration of entire faunas or biofacies. Recently, Patzkowsky and Holland (1996) and Holland (1997) have documented a similar pattern within the Middle and Upper Ordovician of eastern North America. The “Richmondian invasion” (Holland, 1997) involved the reappearance of a number of lineages that were displaced from the region of the then-tropical area of present day Arctic Canada. Evidently, longer-term secular variations in climate and/or water chemistry forced these organisms out of eastern North America coincident with a second tectophase of the Taconic Orogeny. However, later, when oceanographic conditions were restored to more nearly their pre-Taconic condition, some of the lineages were able to reinvade.

Long-term faunal recurrence appears to be a response to factors other than simple sea-level variation, such as climatic changes. As with incursion epiboles, preliminary observations indicate that major faunal migrations are associated with highstands of major second-order sequences, typically occurring just above major black shales (Brett and Baird, 1995, 1997). Thus, the periods of faunal outage in a region may be initiated by particularly extreme sea-level rises that coincide with climatic change. During these times, shallower-water biofacies are displaced great distances by faunal tracking and are introduced into a new region. At the same time, climatic or other non-depth related factors become sufficiently altered in the basin of faunal origination such that, when appropriate bathymetric conditions return to the area, it is no longer hospitable to many of the original suite of species, which become extinct, at least locally. A new fauna appears in most biofacies, derived from tolerant holdovers, newly evolved derivatives of these endemics and, in some instances, a large proportion of immigrant taxa, themselves displaced by the same event from their original provinces. In some cases, later environmental changes may partially reverse the pattern, enabling some of the displaced faunas to reinvade their original territory.

The phenomenon of large-scale faunal migrations clearly requires more in-depth study. It may be at the root of some of the abrupt faunal overturns that bound blocks of
relative stasis or ecological-evolutionary subunits documented by Brett and Baird (1995; see below).

**ITERATIVE EVOLUTION AND SEDIMENTARY CYCLES**

Stasis within and between sedimentary cycles (e.g., Hallam, 1978) suggests that anagenetic change is an exceptional response to fluctuating sea level. Sheldon (1993) has argued that anagenesis may be characteristic of stable, monotonous environments, whereas those with frequent fluctuations favor stasis. Presumably, organisms must remain relatively unspecialized to cope with environmental fluctuations. However, some case studies have documented long-term anagenetic changes that appear to relate to sedimentary sequences.

The occurrence of iterative evolutionary patterns within several sedimentary cycles offers the potential for testing for relationships between evolutionary pattern and environmental change (Fig. 8). For example, Bayer and McGhee (1985) observed iterative cycles of heterochronic morphological change (peramorphosis) in Middle Jurassic ammonites from Klupfel-type sedimentary cycles in Germany. Small, ribbed, evolute, and highly variable ammonites typical of the heterolithic, storm-dominated facies of transgressive portions of the cycles were replaced by large, involute, and less variable forms in "monotonous" mudrocks in the highstand portion of each cycle. The authors attribute the initial small, paedomorphic forms to adaptation in stressed environments near the regressive maximum or lowstand; local heterogeneities favored a high degree of morphological variability. Conversely, more uniform conditions of the highstand favored the less variable peramorphic forms. This pattern agrees with the prediction of Hallam (1978) that evolution of ammonoid species during regressions involved r-selection, favoring paedomorphs, while k-selection operated during transgressions. With one exception, Bayer and McGhee (1985) observed that the founders of these lineages did not arise within the basin, but immigrated from Tethyan sources episodically during sea-level lowstands.

Based on this case study, Bayer and McGhee (1985) also proposed a general model for evolution related to sea-level fluctuation in local basins. They postulated that restriction and fragmentation of habitat area occurred during regressions (lowstands), leading to preferential extinction and replacement of offshore species. Bayer and McGhee postulate that, if the basin was isolated, in situ evolution might be accelerated at this time by allopatric speciation. Similarly, Kauffman (1977) postulated high rates of species evolution during shallowing intervals. However, Bayer and McGhee also suggest that, if a basin had connections to other areas, replacement by immigration of "preadapted," exotic species might preclude local evolution because immigration rates would far exceed evolutionary rates. This model has very important implications for patterns of extinction and speciation in stratigraphic sequences. It needs to be very carefully tested by detailed studies of faunal patterns in local basins.

**MACROEVOLUTION AND SEQUENCE STRATIGRAPHY**

Conditions responsible for producing sedimentary sequences may also be tied to major evolutionary bioevents. Many authors have documented correlations between large-scale extinctions/evolutionary radiations and fluctuations in relative sea level (Moore, 1954; Newell, 1967; Johnson, 1974; Ramsbottom, 1981; Jablonski, 1980, 1985, 1986; Fischer, 1986; Hallam, 1987, 1989, 1992). There are a number of theoretical arguments for such a relationship, mainly related to species diversity-habitat area relationships derived from study of island biogeography (MacArthur and Wilson, 1967; Simberloff, 1974; Schoffeniels, 1974).

The most obvious connection is undoubtedly that of sea-level fall and major extinction. As a result of the area effect (Simberloff, 1974; Schoffeniels, 1974), substantial drops in sea level may produce major habitat-area reduction and stress in marine communities, resulting in mass extinctions. Jablonski (1986) and Hallam (1989, 1992) have stressed that sea-level drop is the most pervasive environmental correlate of major mass extinctions. Many of the larger mass extinctions show some element of association with sea-level drop. Sea-level lowstands and regression should be expected to produce major erosional surfaces that bound large-scale depositional sequences. Several of the major crises in life history, notably the late Ordovician (Ashgill), Permo-Triassic, and Cretaceous-Tertiary extinctions are associated with very major drops in global sea level. Such
extinctions are, thus, associated with major sequence boundaries of second- or third-order cycles.

However, few of the largest sea-level drops, such as those that form Sloss’s (1965) megasequence boundaries, are associated with mass extinctions. Many other third-order unconformities recognized by seismic stratigraphers, such as the very major Oligocene sea-level lowstand, also do not coincide with mass extinction. Jablonski (1985) argued that even complete draining of modern continental shelves would not produce major extinction because offshore oceanic islands would still harbor plentiful species from which continental shelf seas could be repopulated. Hence, even rather major regressions may not directly impact organisms as predicted by the area-effect model. However, Johnson (1974) has stressed that, following times of extensive cratonic flooding by shallow epicontinental seas, organisms may suffer far greater extinction during sea-level drop. Not only do relatively minor sea-level lowstands expose vast areas, but under these conditions organisms may have become specifically adapted to local conditions in the epeiric seas; such “perched faunas” may be especially vulnerable to habitat loss. Thus, conditions prior to the regression may be most critical in determining its effect. Moreover, some sea-level drops may rather be associated with major climatic change, especially cooling, which actually produced the observed extinctions (Stanley, 1984, 1988). Evolution of widespread, stenotopic cool-water faunas may also occur during “icehouse” times or associated with major regressions. This phenomenon is well exemplified by the widespread Late Ordovician Hirnantia fauna that proliferated after the Ashgill extinctions (Brenchley, 1989).

Conversely, a number of studies have pointed to the association of transgressions and evolutionary radiations of shallow-marine organisms (Moore, 1954; Kauffman, 1977; Hallam, 1978; House, 1985). Flooding of continental areas by shallow seas should increase habitable ecospace and favor evolution of stenotopic organisms (cf., the “perched fauna” hypothesis of Johnson, 1974). Warming global temperatures and weakening climatic gradients during transgressions also may favor evolution of stenotopic faunas (Kauffman, 1977; Fischer, 1986).

Several authors have documented a relationship between punctuational faunal changes and sea-level fluctuations. For example, Hallam (1987, 1992) has documented a close correspondence of extinctions with sea-level lowstands and radiations with transgressions in Early and Middle Jurassic ammonite families. Likewise, Dockery (1986) relates major turnovers in Paleogene molluscan faunas with regressions that produced sequence boundaries in the Gulf Coastal area. Although Hansen (1987) claimed no correlation between molluscan extinction and sea-level for the same strata, a pattern of foraminiferal extinctions with sequence boundaries comparable to Dockery’s molluscs was observed by Gaskel (1991). However, the sharpness and apparently synchronous nature of these extinctions may be partly an artifact of the unconformities (Holland, 1995). Bayer and McGhee (1985) documented repeated patterns of local extinction, followed by in situ evolution and immigration, during lowstands in Mesozoic third-order cycles.

On the other hand, other studies have revealed no relationship between faunal change and sea-level fluctuation. For example, Leckie et al. (1992) found that important turnover events in Cretaceous plankton and reefs tended to occur within sequences and not at their boundaries. McGhee (1991, 1992) notes that most previous studies relating evolutionary patterns to sea-level have been qualitative. In detailed statistical studies, McGhee compares rates of extinction and diversification for Devonian brachiopods in New York to the sea-level curves of Johnson et al. (1985). He concludes that there is no correlation between relative sea-level change (McGhee, 1991) or rate of sea-level change (McGhee, 1992) and patterns of extinction or diversification (although the data on which this study was based [Dutro, 1981] are incomplete, and, as noted above, some faunal overturn events in the Appalachian basin do appear to be linked with transgressions). Clearly, there is a need for many more such critical studies. Thus, despite probable correlation in some cases, no simple, predictable relationship exists between sea-level lowstands, sequence boundaries, and mass extinctions.

A further relationship between sea-level effects and macroevolution involves major transgressions and extinctions. Episodes of widespread bottom-water anoxia in shallow seas and oceanic anoxic events (OAE; Arthur and Schlanger, 1979) very commonly correlate with maximum sea-level highstands (Hallam and Bradshaw, 1979; Wignall and Hallam, 1991; Wignall, 1994). These anoxic events may cause waves of extinction that propagate from offshore basinal areas to shallow shelves as the extent of the anoxic water column expands (Hallam, 1987, 1992). Area-reduction effects again pertain, as major tracts of shallow seafloor become anoxic and uninhabitable. However, in this case, offshore low-oxygen adapted organisms may show differential survivorship. These extinctions would be predictably associated with maximum flooding surfaces or condensed sections.

Excellent examples of such highstand-related extinctions are documented by Kauffman (1984) and Elder (1987) for the Cretaceous Cenomanian-Turonian and Turonian-Coniacian extinctions. In both cases, major extinction of even eurytopic forms was associated with an anoxic event during or just before peak transgression. The extinctions followed periods of equitable conditions in the early- to mid-transgression, which favored establishment of high-diversity faunas. These extinctions were then followed by major faunal turnovers and further extinctions coinciding with stresses during regression. Kauffman (1984) noted the importance of ameliorated conditions prior to the anoxic events that “set the faunas up for the kill.” Although differing in details, both the Albian-Cenomanian and terminal Cretaceous extinctions followed somewhat similar patterns (Kauffman, 1984).

A comparable pattern has been found for local extinctions and faunal turnover events in the Devonian of the Appalachian Basin (Brett and Baird, 1995). For example, the demise of the Eifelian Onondaga fauna and appearance of the well-known Givetian Hamilton fauna is associated with a major eustatic sea-level rise and an interval of widespread anoxia (Brett and Baird, 1996); this coincides with the global Kakac-oatomari bioevent (Walliser, 1986a,b, 1990; Boucot, 1986; 1990a,b). Similarly, the abrupt loss of much of the Hamilton fauna occurs with another eustatic highstand and widespread low oxygen conditions, and coincides with the global Pharciceras bioevent.
(House, 1985; Boucot, 1990b). In each case, a major eustatic rise and anoxic event is associated with local extermination of more than 70% of species, accelerated in situ evolution, and immigration. The Kacak event in the Appalachian Basin follows a pattern similar in detail to the Cenomanian-Turonian event documented by Kauffman (1984), in showing the introduction of a temporary, probably warm-water fauna at or near peak transgression that was subsequently extinguished and replaced by stable fauna. Likewise, the Frasnian-Famennian extinction has been associated with two intervals of widespread anoxia—the lower and upper Kellwasser events (Schindler, 1990)—perhaps but not unquestionably associated with maximum flooding surfaces (see McGhee, 1992).

The situation is clearly complex and not entirely predictable, but a number of faunal overtures do coincide with lowstands or transgressive maxima. However, each case must be carefully evaluated on its own merits. Far more detailed studies, such as those of Kauffman (1984; 1986) and Elder (1987), must be done before any more definitive generalizations can be made. However, at least the sequence model provides an important framework within which to test these ideas.

CONCLUSIONS

(1) Paleoecology has a dual relationship with sequence stratigraphy. Fossils provide very important tools for reconstructing patterns of environmental change that relate to sequence-forming processes; and sequence stratigraphy provides a predictive framework that facilitates recognition and interpretation of patterns of biotic change in the geologic record.

(2) Paleontological cues to sequence interpretation include several parameters. Fossils provide indicators of absolute and relative depth; fluctuations in body and trace fossil associations or “communities” may permit recognition of cycles even in seemingly monotonous mudrock facies. Certain types of organisms are sensitive indicators of low turbidity and sedimentation rates; trace fossil concentration and crosscutting relationships may aid in recognition of condensed intervals and submarine erosion surfaces. Variations in substrate consistency, that may, in turn, relate to changes in sedimentation rate, can be judged from the occurrence of fossil taxa known to be substrate selective. Traces and body fossils also may elucidate fluctuations in benthic oxygenation that relate to sea-level variation.

(3) Temporal variations in fossil assemblages (“communities”) can be interpreted within the framework of sequence stratigraphy. Long-term (10's to 100's of Ka) community replacement should be distinguished from short-term ecological succession, although these two processes, operating at different scales, may display significant parallels that relate to position within onshore-offshore gradients of disturbance frequency.

(4) The recurrence of highly similar fossil assemblages in analogous portions of sedimentary cycles indicates that associations of species that require particular combinations of depositional environments persist with relatively little change through long intervals of time. These associations appear to shift laterally over considerable distances during intervals ranging from a few thousands to perhaps a few millions of years. Rather than adapting to the stress of changing environments, marine organisms most commonly appear to track their favored environments. Provided that the lateral migration of these environments is not too rapid, or that these environments do not disappear altogether from the local basin, most organisms appear to be able to keep up with the shift of environments produced by sea-level fluctuation.

(5) Similar rates of sediment accumulation during transgressions and highstands (including regressions) may lead to nearly symmetrical cycles of faunal habitat tracking. Many asymmetries in tracking can be readily interpreted as either artifacts of incomplete preservation of facies transitions (e.g., at sequence boundaries or surfaces of maximum starvations), or as real biotic responses to fluctuating sedimentation rates, turbidity, and substrates within sedimentary cycles. Sedimentation rates are much lower in proximal areas during transgressive phases, due to coastal sediment entrapment, than during late highstands or regressions. Fossil assemblages vary accordingly. Low sedimentation conditions or special substrates formed in condensed intervals may permit proliferation of normally rare species, leading to ecological epiboles. Moreover, some eurytopic species may not track but remain in a particular area and show ecophenotypic responses, for example, to changing substrate conditions.

(6) Some faunal replacements involve immigration of species into a local basin from other basins or provinces. These incursions may be short-lived (but geographically widespread) events, involving a few species (incursion epiboles), or wholesale influx of “exotic” associations. In both cases, there appears to be an association with transgressive highstands. This relationship may involve climatic changes (typically warming) indirectly related to the highstand, or the opening of dispersal routes because of high sea-level stands. However, in some cases, incursions may also be associated with unusual conditions during lowstands.

(7) In situ evolution is a less common response to sequence-generating environmental changes. Lateral shifting of tracking biotas, or incursion of immigrant species, appears to occur at a much higher rate than evolutionary adaptation. However, Bayer and McGhee (1985) postulate that allopatric speciation may result from habitat fragmentation during regressions in some isolated basins.

(8) Patterns of large-scale evolutionary radiation and mass extinction may be related in complex ways to large-scale fluctuations of sea level and related effects that also generate depositional sequences. Many empirical and theoretical studies link extinctions to reduction in habitat area or climatic stress (typically cooling) during major lowstands. Transgressions generate increased habitat space and ameliorated climates that may favor evolutionary radiations. However, loss of habitable seafloor may result from the spread of bottom-water anoxia during transgressions, and produce waves of extinction from deep-to-shallow water environments. Hence, bioevents commonly may
be associated with either sequence boundaries or sur-
faces of maximum flooding. Indeed, major stable eco-
logical-evolutionary units may be bounded at strati-
graphically important discontinuities. However, some
studies have found little or no relationship between
macroevolution and sea-level fluctuations, and many
of the largest sequence-bounding unconformities and
flooding surfaces bear no evidence of dramatic bio-
events. The relationship between sequence stratigraphy
and macroevolution is obviously complex and multi-
factorial. Nonetheless, it warrants considerably more
detailed quantitative study.

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