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RESPONSE OF SHALLOW MARINE BIOTAS TO SEA-LEVEL FLUCTUATIONS: A REVIEW OF FAUNAL REPLACEMENT AND THE PROCESS OF HABITAT TRACKING

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ABSTRACT

Associations of fossil genera and species commonly display repeated and predictable patterns of change in stratigraphic sections. These changes exhibit some analogies with the phenomenon of ecological succession but are longer-term allogenic temporal changes, occurring over time scales of tens to hundreds of thousands of years, that should be referred to as biotic (faunal-floral) replacement. Habitat tracking is one of a suite of possible mechanisms of biotic replacement, but one that may be important in certain marine settings. Evidence of tracking includes (1) recurrence of similar replacement series of differing age; (2) mirroring of vertical replacement of faunas by lateral gradients of species associations along single time planes; (3) the occurrence of similar gradient transects at different time planes; (4) the correlatability of highs and lows of quantitative faunal curves (e.g., variations of detrended correspondence analysis scores) at different localities despite offsets of absolute scores; and (5) the high fidelity recurrence of stenotopic species in particular associations representing narrowly defined environments. The degree of ecological fidelity (e.g., similarity of species richness, guild structure) that is maintained during tracking is variable. Recurrent assemblages in different cycles, separated by as much as several million years, can be very similar in terms of species composition and trophic structure. Common species, however, may show significant differences in rank and relative abundances. This evidence indicates individualistic tracking of preferred habitat by various species. In shallow-shelf and ramp settings, sea-level fluctuations may produce approximately symmetrical patterns of biotic replacement where biofacies are arrayed typically in elongate belts parallel to depositional strike. Asymmetries, however, are common and may result from variations in sediment supply during sea-level fluctuation. Hence, the low siliciclastic input typical of transgressions predictably favors those organisms that require lower sedimentation or turbidity and perhaps firmgrounds to hardgrounds, whereas the regressive half cycle at analogous depths favors more eurytopic organisms that tolerate or prefer higher sedimentation or turbidity. The phenomenon of tracking may be of considerable importance in evolutionary paleoecology. Tracking implies that species commonly respond to long-term physical changes, not by adaptation, but primarily by migration of species to preferred habitats, if the rate or magnitude of environmental change is not too great. Provided that the same basic environment existed through time, despite lateral shifting by up to hundreds of kilometers, most species of benthic invertebrates were capable of surviving with little or no evolutionary change. Tracking may be the primary basis of patterns of morphological stasis, as well as relative stability in biofacies richness, composition, and trophic structure.

INTRODUCTION

This paper reviews patterns and definitions of temporal biotic change in shallow marine biofacies. We review patterns of long-term biotic replacement attributed to the process of tracking, present general evidence, and pose potential tests for tracking. We also discuss deviations from idealized Waltherian tracking models and their probable causes and, finally, consider the implications of habitat tracking for evolutionary paleoecology and biofacies stability.

For many years, paleontologists have noted the temporal recurrence of species and assemblages, also termed associations, communities, paleocommunities, community types, and biofacies, through stratigraphic successions (Johnson, 1964, 1972; Ziegler, 1965; Ziegler et al., 1968; Anderson, 1971; Cisne and Rabe, 1978; Cisne et al., 1984; Johnson et al., 1985; Springer and Bambach, 1985; Brett et al., 1990; Jackson, 1994a, 1994b). Renewed interest in this relationship has been fostered by the development of the sequence-stratigraphic paradigm (Vail et al., 1977, 1991; Van Wagoner et al., 1988; Wilgus et al., 1988; Witzke et al., 1996), which provides a temporally constrained framework within which to interpret various paleoecologic and evolutionary events, particularly in permitting precise evaluation of the timing of events and understanding how processes associated with sequence development influence animal communities (Brett, 1998). The processes of sea-level, climate, and sediment-supply fluctuation have strong biological impacts, controlling spatial distribution of organisms at a variety of scales and influencing patterns of immigration, origination, and extinction (Bennett, 1990; Valentine and Jablonski, 1991; Roy et al., 1994, 1996; DiMichele et al., 2004). Bathymetric and sedimentologic factors, in particular, exert major controls on the distribution patterns of shallow marine benthic organisms. A phenomenon observed in the modern realm and inferred from the fossil record is the zonation of benthic assemblages both along and across depositional strike (Boucot, 1975; Abbott and Carter, 1997; Scarponi and Kowalewski, 2004; Hendy and Kamp, 2007). The predictable recurrence of depth-related benthic assemblages (e.g., Ziegler, 1965; Ziegler et al., 1968; Boucot, 1975, 1982; McKerrow, 1979; Boucot and Lawson, 1999) has provided a useful application of paleontologic data to analysis of sedimentologic and stratigraphic patterns.

Predictably recurring stratigraphic patterns of fossil distribution can be commonly related to small- and large-scale sedimentary cycles. Indeed, this notion of cyclic recurrence is fundamental to identification of biofacies. For purposes of discussion, we prefer the term biofacies to community; the latter term has been fraught with ambiguity and may carry a connotation of a discrete, structured entity. Biofacies, as discussed herein, are generalized groupings of taxa that characterize particular environments and, in some cases, represent segments of biotic gradients. Biofacies represent the recurrence of similar groups of taxa through stratigraphic successions and may persist for prolonged periods (up to a few million years) before being reorganized or replaced during major environmental perturbations.

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The temporal pattern of biotic change recorded in particular vertical stratigraphic sections has been referred to as community replacement (Kauffman and Scott, 1976; Miller 1986, 1988, 1990a, 1990b). It has been suggested that replacement commonly reflects a process that has been termed habitat tracking (Miller, 1990b; Brett, 1998).

This paper focuses on tracking as an alternative to nontracking modes of biotic replacement emphasized in other recent studies (Bennett, 1990; Jackson and Overpeck, 2000; DiMichele et al., 2004). Habitat tracking at the scale of biofacies is only one of the various processes of biotic replacement and probably does not apply to most continental and many marine environments. We suggest, however, that it may be a common pattern in certain settings that are the purview of this special volume: shallow marine ramps and shelves subject to gradual fluctuations in sea level. Habitat tracking is one, possibly important, mechanism to generate recurrence in associations that has implications for the type and rate of environmental change. Eldredge (1995, 1999) argued that habitat tracking might be the most important causal mechanism for evolutionary stasis (see also Gould, 2002, p. 880–881).

Many questions remain with respect to the issues of recurrence and tracking. To what degree are aspects of species diversity (richness), guild structure (*sensu* Root, 1965), species-list, and relative or rank ordering maintained in successive appearances of a particular biofacies? Can these attributes of ecological structure, taxonomic composition, or abundance structure be maintained through a major physical perturbation? Can gradients of species or genus distribution persist through long periods of time, or do they fluctuate continually? Answers to these questions speak to important issues in evolutionary ecology. For example, are communities tightly knit entities with a stability resulting from biotic interactions, as per the Clementsian view (Clements, 1916), or merely collections of independently responding species that co-occur because of similar environmental tolerances, as in the Gleasonian perspective (Gleason, 1926)? Perhaps it is more important to determine the situations under which species and species associations may persist and track shifting environments and those under which they do not, for herein may lie an important control on rates of evolution.

TEMPORAL BIOTIC CHANGES IN RESPONSE TO ENVIRONMENTAL CHANGES: BIOTIC SUCCESSION AND REPLACEMENT

Scales of Temporal Biotic Change

Temporal changes in composition of biofacies occur at varying scales (Table 1). Numerous terms, including community succession (e.g., Donahue et al., 1972; Johnson, 1972; Donahue and Rollins, 1974; Bretsky and Bretsky, 1975; Walker and Alberstadt 1975), community replacement, or biofacies replacement (e.g., Rollins et al., 1979; Brett, 1998; Patzkowsky and Holland, 1999), and community reassembly (e.g., Miller, 1986; Miller and Dubar, 1988), have been used by paleontologists to describe such temporal changes observed in the sedimentary record. The following section reviews the different temporal levels of biotic change and suggests a slightly revised terminology.

Biotic Succession.—Short-term biotic change involving compositional variation on the scale of an individual bed or sediment body may be termed succession (*sensu lato*). Such change involves physical or biotic alteration of the local environment leading to systematic changes in the biota and operates in ecological time frames of tens to a few hundreds of years. Walker and Alberstadt (1975) distinguished between autogenic succession (which is succession *sensu stricto* of most ecologists; e.g., Elton, 1933; Odum, 1971; Pickett, 1976; Connell and Slaytor, 1977), involving environmental changes brought on by the activities of colonizing of organisms themselves, and allogenic succession, in which biotic changes are brought on by external, environmental controls (Walker and Alberstadt, 1975).

Short-term biotic changes, including true (autogenic) succession, are rarely resolvable in marine sections given the low rates of background sedimentation and mixing effects of bioturbation (Schindel, 1980, 1982; Sadler, 1981). Episodic sediment accumulation, however, may provide snapshots of seafloor communities in different stages of succession (Taylor and Brett, 1996) that permit indirect reconstruction of successional patterns. Plausible cases in which several successive seres are preserved include examples of reefal succession (Walker and Alberstadt, 1975). Allogenic succession may include evidence for change from soft- to firm- to hardground communities resulting from progressive lithification of the seafloor (see review by Wilson and Palmer, 1992). Taphonomic feedback represents a special case of short-term change, involving both autogenic (e.g., skeletal production) and allogenic (e.g., storm aggregation) aspects in which the accumulation of skeletal debris makes the seafloor disadvantageous to burrowing infauna and favors encrusting epifaunal dominated communities (Kidwell and Jablonski, 1983). Larger, allocyclic processes may, in turn, mediate all of these types of short-term biotic change. For example, hardgrounds, shell grounds, and reefal buildups may all be promoted by low rates of sedimentation during sea-level rise (see McLaughlin and Brett, 2007).

Biotic Replacement.—Initially, paleoecologists made an analogy between large-scale temporal changes and the ecological notion of community succession (Johnson, 1972; Donahue and Rollins, 1974; Bretsky and Bretsky, 1975; Rollins et al., 1979). For example, the stratigraphic distribution of Ordovician invertebrate fossil associations observed through more than 800 m of cyclic sediments in the Nicolet River Valley was termed long-term succession by Bretsky and Bretsky (1975), and the stepwise changes were considered successional seres.

Both the time scale and processes involved in these changes were subsequently recognized as being completely different from those associated with succession as defined by neontologists (e.g., Gould, 1980; McCall and Tevesz, 1983; Brett, 1998). For example, the changes observed by Bretsky and Bretsky (1975) occur through tens to hundreds of meters of stratigraphic section and probably respond to cyclic processes operating over thousands or tens of thousands of years. Nevertheless, there are interesting parallels between seres of short-term succession on mud bottoms and the longer-term overall patterns. Notably, the pioneer assemblages of successions following storm disturbances in shallow water areas may mimic stable fossil associations in deeper, dysoxic environments typical of the lower portions of shallowing-upward cycles (Taylor and Brett, 1996). This is true presumably because stressed and fluctuating conditions in deeper dysoxic basins favored eurytopic, generalized organisms that occur broadly in many environments—of the same sorts that formed pioneers in successions following disturbances in shallow-water settings. Moreover, fluctuating oxygen levels in dysoxic settings frequently downgrade successions and maintain communities at a pioneer sere.

Thus, while the long-term process of biotic replacement may in some ways mirror processes seen in ecological succession, it is not the same thing, and the term community replacement was eventually substituted for the term long-term allogenic succession (Walker and Alberstadt, 1975; Rollins et al., 1979; Miller, 1986, 1990a, 1990b; Table 1). The terms faunal replacement, floral replacement, or biotic replacement are preferred to community replacement because of the controversies surrounding the definition of the term community (see Springer and Miller, 1990).

The vertical changes of biotas in sedimentary cycles occur generally at time scales of thousands to hundreds of thousands of years, the same scale as such processes as sea-level and climatic fluctuations; the two are often closely related as evidenced by lithofacies and biofacies changes in cycles (e.g., Bennett, 1990, 1997; Cateneaunu, 2002; Coe, 2003). It should be noted that not all stratigraphic changes in biotic composition qualify as biotic replacements. Discontinuities ranging from subtle diastems to larger disconformities may juxtapose dissimilar fossil assemblages that were not adjacent or contemporaneous. These changes in fossil composition, termed heterochronous replacements by Rollins et al. (1990), are an artifact of missing section and are typical of sequence boundaries and flooding surfaces of depositional sequences (Holland,

TABLE 1—Terminology of biotic replacements.

Time scale	Stratal pattern	Inferred process	Examples
Short term (ecological scale):			
Within bed/bioherm (10–10^3 yrs)	Succession	Autogenic succession Allogenic succession Taphonomic feedback	pioneer-climax seres in reefs softground to hardground biotas soft substrate-shell ground
Intermediate term:			
Bed scale (10^3–10^4 yrs)	Gradational replacements	Habitat tracking	gradual change from one biofacies to next
	Disjunct replacements	Disassembly-reassembly	abrupt change from one biofacies to different one
Formation scale (10^4–10^5 yrs)	Replacement series	Habitat tracking Dissasembly-reassembly	pattern involving sequential biofacies replacements
	Symmetrical series	Habitat tracking	symmetrical pattern of replacement with mirror image recurrence of biofacies
	Asymmetrical series	Habitat tracking Disassembly-reassembly	asymmetrical pattern of gradual biofacies replacements without return to same end-point
Long term (evolutionary scale):			
(10^4–10^6 yrs)	Disjunct biotic turnover	Immigration, evolution Emigration, extinction	part or all of preexisting biofacies gradient is replaced by new biofacies not previously present in local basin

1996). True biotic replacement can only be documented in continuous stratal sections.

Patterns of Biotic Replacement

Gradual and Disjunct Replacement.—The vertical stacking of changing fossil assemblages may record a gradual or piecemeal changeover from one portion of a gradient, of species, or of en echelon replacement *sensu* Miller (1990a), or it may be abrupt in a true, biological sense, despite conformity in the strata. Miller (1990a) identified such abrupt changes as catastrophic turnovers; such replacement patterns are herein referred to as disjunct replacement (Table 1). These abrupt changes almost certainly record a fairly major and rapid environmental change, even if the physical stratigraphic record appears unbroken and the facies monotonous.

Replacement Series.—In many cases, gradual vertical biotic replacement, or gradational replacement, involves a series of three or more biofacies, which is referred to herein as a replacement series. A replacement is simply a vertical change in biofacies and may or may not reflect Waltherian juxtaposition of adjacent biofacies. A critical question to be considered in evaluating long-term stability is whether replacement series of different times and places show a predictable stacking order of successive biofacies.

The vertical pattern of replacement series through a local cycle may appear nearly symmetrical, with more or less mirror-image recurrence of fossil assemblages on either side of the cycle center. Brett (1998) termed this pattern symmetrical tracking, but, as tracking implies a process, rather than a pattern, we substitute the term symmetrical replacement for such vertical patterns. Conversely, in asymmetrical replacements, the patterns of biotic replacement may be quite dissimilar in different portions of a cycle; that is, the regressive half cycle may show a very different pattern from the transgression. Some asymmetries are a stratigraphic artifact produced by missing section owing to erosion or condensation. Others, however, are based on environmental asymmetries during depositional cycles (Rollins et al., 1979, 1990; Brett, 1998).

Biotic Turnovers.—A special type of disjunct replacement occurs at the boundaries of ecological-evolutionary units (Brett and Baird, 1995; Sheehan, 1996). This type of replacement frequently involves the appearance of a suite of species not previously seen in the basin via immigration or new evolution, as well as loss of taxa by emigration, and extinction. This higher-level disjunct replacement is commonly referred to as biotic turnover. While such replacements are intrinsically interesting, we do not consider them further in this paper.

MECHANISMS OF REPLACEMENT

Gradual, en echelon replacement connotes a pattern of stratigraphic change in fossil assemblages, encompassing hundreds to thousands of years and recording environmental fluctuations, typically sea-level cycles. Examples of biotic replacement are abundant in Plio–Pleistocene sedimentary sequences (e.g., Bennett, 1990, 1997; Kitamura et al., 1994; Abbott and Carter, 1997; Dominici, 2001; Hendy and Kamp, 2004, 2007; DiMichele et al., 2004), where they result from glacioeustasy, occurring through time spans of 41–100 ky.

Disassembly-Reassembly

Piecemeal reassembly of faunal associations recruited from various local species pools appears to typify certain types of biofacies in particular settings (Miller, 1986, 1990a, 1990b; Buzas and Culver 1994, 1998). For example, it is clear that replacements of continental mammal and plant assemblages in successive Pleistocene glacial-interglacial cycles involved strongly individualistic behavior and that successive communities typically involved substantially different combinations of species, including species that are rarely, if ever, found living together in recent times (non-analogue assemblage; see Bennett, 1990; Graham et al., 1996; Jackson and Overpeck, 2000). Similarly, Valentine and Jablonski (1993) and Stanton and Dodd (1997) document substantial flux in species composition in Plio–Pleistocene marine molluscan assemblages from seemingly analogous environments that may represent essentially continuous reorganization of associations from changing species pools. An implication of these studies is that most species exhibit highly individualistic behavior and, moreover, may occupy a greater range of environments than those realized during a point in time, such as the present day, and form a wide array of different associations with other species.

This view is in line with metacommunity models in which geographical patterns of species are shaped by chance appearances and disappearances of local habitat patches (see the review in Jackson and Overpeck, 2000). Metacommunity models can be treated as null models against which patterns of nonrandom taxonomic associations can be identified. In at least some cases, the models do not appear to predict distribution patterns of real species (Harrison, 1994). Harrison (1998) argued that there is no support for metacommunity models of community assembly: ‘‘Instead, it appears likelier that species are present in most of their habitats most of the time’’ (Harrison, 1998, p. 29). This view is in accord with the fossil record of certain recurring assemblages in ancient marine environments

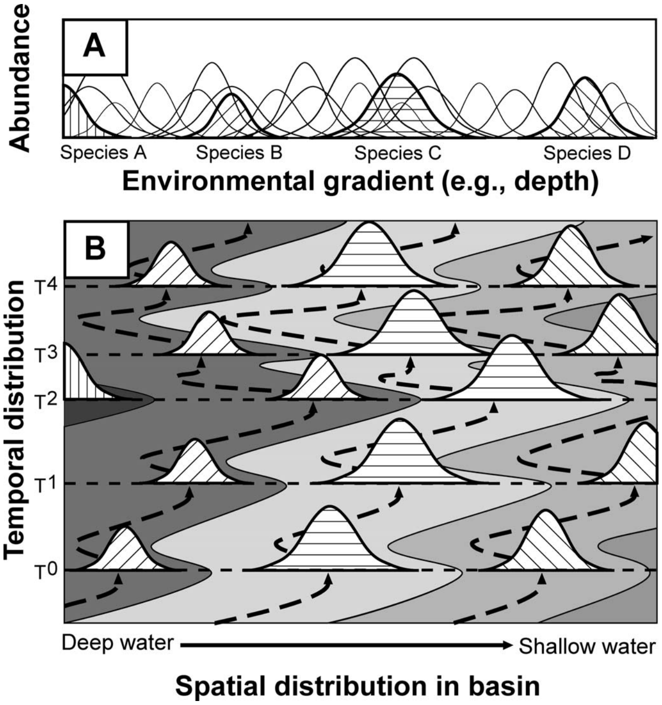

FIGURE 1—Conceptual model of tracking based on the concept of Gaussian distribution of species along an environmental gradient. A) Distributions of various species along the depth gradient. Note that biofacies could be recognized as the overlapping ranges of several species along arbitrary segments of the gradient; no interactions among species are implied. The four species highlighted are shown in time-geography diagram below. B) Time-geography plot showing tracking of four species through several shallowing-deepening cycles, assuming that relative abundances and positions of each species along the gradient are maintained through time.

and the concept of tracking. Conversely, there is no major disagreement with metapopulation models (see McKinney and Allmon, 1996) that postulate local decimation of populations followed by reestablishment from nearby sources or larvae within the water column. It is certainly plausible that metapopulation dynamics of this type are ongoing but are simply not resolvable in most time-averaged assemblages; this kind of change occurs at the scale of biotic succession, rather than biotic replacement.

Habitat Tracking

Replacement series in some marine benthic assemblages commonly display predictable recurrence of species groups or associations. Although perfect recurrence of relative abundance, species composition, or richness is observed rarely (Miller, 1990b; Bennington and Bambach, 1996), there are often strong similarities between samples of markedly different age that seemingly derive from similar environments, at least in terms of water depth and sedimentary regime. For example, Brett et al. (2007) document the recurrence of 60%–80% of species in samples of diverse Middle Devonian biofacies that span approximately 5 myr and also show the same stacking order in several cycles. Arguably, when such predictable replacements occur repeatedly in regular succession-like order in sedimentary cycles, as in Bretsky and Bretsky's (1975) famous example, habitat tracking appears as a plausible and parsimonious explanation.

Habitat tracking is defined here as the lateral migration of species or biofacies in response to shifting environments (Fig. 1). The concept of habitat tracking should be distinguished carefully from biotic replacement, as the latter denotes a pattern, while the former represents an inferred process. It is further implied that tracking involves temporal and typically spatial continuity in distribution of populations of particular species or species associations within a local depositional basin during migration, rather than local extinction and recolonization from outside sources.

Species-Level Tracking.—It is also necessary to make a careful distinction between habitat tracking at the level of particular species, as opposed to tracking of associations of species or biofacies, which we refer to as biofacies-level tracking. At a species level, tracking implies that populations typically do not remain in one site and acclimate or adapt in the face of gradual environmental change or change habitat tolerances through time. Moreover, the species need not be recruited from external sources. Obviously, each species has a particular range of tolerance for environmental parameters. Most larger organism species probably do not evolve quickly enough to keep up with changing environments by adaptation and, thus, have only the option of lateral shifting (Jackson and Overpeck, 2000). The persistence of many species, stasis, implies that habitat tracking at a species level is a significant phenomenon. Species-level habitat tracking, however, need not result in habitat tracking by biofacies.

Biofacies-Level Tracking.—As noted, biofacies-level tracking is only one possible process among several that may result in patterns of biotic replacement. Other possibilities include (1) complete disassembly and reassembly of varying combinations of species from metapopulations, resulting in nonrecurrent replacement series, and (2) tracking of some species, but not a majority, with variable reassembly of remaining species. If species are tracking habitats largely independently of one another, then biofacies tracking may occur when only one or two major environmental parameters are changing gradually. If several different environmental factors are changing independently of one another, then varied assortments of species may be formed and reformed through time, as well illustrated in examples of Pleistocene land plants (Jackson and Overpeck, 2000). Conversely, if some biofacies are more tightly structured with numerous biotic interactions, as is possibly the case in some high-diversity reef communities (Pandolfi, 1996), they may track with considerable fidelity, perhaps even in the face of some range of fluctuation in several physical parameters.

At the level of species associations, tracking implies that the compositions of biofacies assemblages are relatively persistent through time; rank and relative abundance of species may or may not be maintained. Although it is possible that the local extermination of species followed by reassembly could lead to closely recurrent assemblages under very similar environments (Jackson and Overpeck, 2000), when close recurrence is seen at multiple successive cycles, persistence and tracking of associations is likely.

Habitat tracking does not imply that species form discrete, well-bounded communities (e.g., Aronson and Plotnick, 1998). Rather than forming discrete communities, marine benthic species typically show gradients of distribution along environmental clines. For example, species typically show patterns of preferred distribution down a ramp from shallow to deep water, or along a particular bathymetric zone (facies belt) from low- to higher-sedimentation rates (Holland et al., 2001; Webber, 2002; Hendy and Kamp, 2004; Holland and Patzkowsky, 2004). In this sense, a biofacies or community type (*sensu* Bennington and Bambach, 1996) may simply be the sum of segments of particular species gradients (Fig. 1). Quantitatively, biofacies are analogous to clusters of a dendrogram and are often defined as such. Conversely, gradients can be depicted by the continua of ordination (e.g., Holland and Patzkowsky, 2004).

Recurring replacements of biofacies may be conceived of as the shifting of particular parts of the gradient into or out of the frame of reference provided by a local outcrop section (Fig. 1). In fact, the concept of tracking is quite in line with the occurrence of gradients of species composition and says nothing about the cohesiveness of communities. Tracking, however, does imply the persistence of relatively stable gradients of species tolerances through time, especially with regard to depth preferences. In this context, the main test of the validity of tracking is whether patterns of species distribution arrayed along environmental gradients are relatively constant through time and are shifted geographically in response to changing sea level or other extrinsic forcing factors.

Considerable paleontological literature suggests that species maintain nearly constant environmental tolerances, particularly relative depth ranges, for prolonged time intervals (see Boucot, 1990, for a review). This is evident in Plio–Pleistocene marine corals and mollusks for which direct comparisons with modern counterparts yield very similar patterns of relative distribution along depth gradients (Pandolfi, 1996; Gardiner, 2001; Scarponi and Kowalewski, 2004; Hendy and Kamp, 2007). Testing the assumption of constancy in habitat preferences and depth tolerances of ancient organisms is difficult. Assuming Gaussian distributions of species along depth gradients, Holland et al. (2001) developed a method for estimating the preferred depth, depth tolerance, and peak abundance of fossil benthic species. Holland and Patzkowsky (2004) applied this methodology to examine the preferred depth, depth tolerance, and peak abundance of various genera through a portion of the Late Ordovician representing ~2–4 myr. They concluded that a majority of common taxa maintain a relatively constant paleobathymetric distribution through time, although they noted several instances in which preferred depths changed within genera through the studied interval. These changes, however, apparently are not found within single species but between different species of the same or related genera. Furthermore, as a complex of environmental parameters probably controls the distribution of species, various combinations of changes may result in modifications of preferred depth.

Olszewski and Patzkowsky (2001) proposed a test of gradient recurrence based on quantitative similarities of distribution of species. For some 51 cyclothems in five sequences in the Pennsylvanian–Permian of the U.S. midcontinent, they found that, while two major biofacies and general gradients of faunal composition within each were recognizable, the specific order of generic association along these gradients was not consistent from cycle to cycle. To date, this test has not been applied in other cyclic recurrences, but it seems probable that the exact order of appearances in cycles may not be recurrent, especially when many species are eurytopic (see Brett et al., 2007) and several parameters control the distributions of most species.

Miller (1990a, p. 41) considered biofacies tracking to be an artifact, as he wrote: ''If habitats recur and if . . . staffing networks remain essentially intact for long intervals of time, ecosystems (as shown by fossil associations) may appear to track shifting environments.'' He argued that most soft-bottom ecosystems familiar to paleoecologists have life spans of 10–10,000 years. While this may be true of the precise local sectors of gradients that might be identified by an ecologist as communities, evidence has been found that general gradients of species occurrence may persist for periods of several million years (Pandolfi and Jackson, 1997; Brett et al., 2007). Miller (1990b) further asserted that benthic communities do not move across the seafloor as well-integrated units that are somehow able to track preferred environments. In his view, a community is much more likely to become disorganized, collapse, and perhaps be reassembled in more or less the same arrangement at a new site. Although a variety of evidence cited herein and elsewhere indicates that many species associations are not tightly integrated entities, we disagree with the notion of frequent collapse and reformulation of these associations along gradients. In most cases there is no evidence for dramatic collapse of a regional ecosystem, although local short-term storm disruption of seafloor patches, as predicted by the successional model of Johnson (1972), may require recolonization (see later sections below). These disruptions, however, do not seem to result in permanent changes in overall biofacies or species gradients; see the discussion of separation of processes acting at different hierarchical levels in Pandolfi and Jackson (1997) and Schopf and Ivany (1998). Time-averaging in most fossil assemblages yields an averaged overview of species occupying a given area through time, frequently smoothing out evidence for such local and short-term disruptions (Schopf and Ivany, 1998).

In shallow shelf seas and foreland basins that have yielded a good deal of the marine fossil record, tracking may occur particularly in response to fluctuations in relative sea level, as indicated by strongly recurrent species associations (biofacies) during transgressive-regressive cycles (Rollins et al. 1979; Bennington and Bambach, 1996; Brett and Baird, 1995; Holterhoff, 1996; Pandolfi, 1996; Pandolfi and Jackson, 1997). That is, collections of species responding to a common environmental signal migrate following their preferred habitat or environmental parameters. In many epeiric ramps, species associations were arrayed in elongate, laterally extensive belts, aligned roughly parallel to shoreline along gently sloping ramps as evidenced by basin analyses and mapping of biofacies (cf. the benthic assemblage concept of Ziegler et al., 1968; Boucot, 1975, 1990; Hurst et al., 1978; see Watkins et al., 2000, for further discussion of changes in the Silurian). Where outcrop belts parallel depositional strike, biofacies may show remarkably little change laterally along time planes (Ziegler, 1965; Boucot, 1975; Brenchley, 1990; Boucot and Lawson, 1999, and examples therein; Brett et al., 2007). Changes in relative sea level of even a few meters should result in shifting of the depth belts for considerable distances up or down a gentle ramp. Maximum rates of glacioeustatic change can be estimated at about 6–8 mm per year, based on evidence of 100–120 m of sea-level rise in the past 15,000 years (see Milliman and Emery, 1968). Such rates of sea-level change are low relative to generation times of benthic invertebrate animals, and it should be possible for most marine species populations to keep up with and shift with their preferred environment. Gradual change in water depth scarcely qualifies as a cause for collapse of an ecosystem. Obviously, for sessile or weakly vagrant organisms migration does not involve mobility of adults but, rather, gradual larval dispersal and differential survival. Figure 1 shows a hypothetical set of species with differing but overlapping depth tolerances. Through time, the mean distribution should shift in response to increasing or decreasing relative depth. Both biofacies and lithofacies respond to sea-level fluctuations.

Tracking inferred from vertical series of biofacies replacements, thus, invokes Walther's principle, often called Walther's Law, of facies stacking (Walther, 1890–1893; Middleton, 1973; but see Soreghan, 1997, for examples of non-Waltherian facies replacement). The vertically superposed biofacies, like the lithofacies themselves, are a manifestation of migration of belts of biofacies that were arrayed laterally to one another at any given time plane. At least some faunal or community replacements may represent tracking and, in these instances, the Waltherian prediction of lateral-vertical relationships is testable.

TESTS FOR TRACKING

The general validity of biofacies tracking is subject to testing, based in part on Waltherian principles. General tests of tracking include (1) orderly recurrence of species and biofacies stacking patterns in cycles of differing place and time; (2) comparisons of vertical series of faunal replacements with lateral gradients of fauna along isochronous transects of the same cycle; (3) comparisons of lateral biofacies gradients along successive time planes; (4) concordance of curves generated by quantitative gradient analysis, for example, detrended correspondence analysis (DCA) in different localities, coupled with offsets in absolute values; and (5) high-fidelity recurrence of endemic stenotopic species in very specific litho- and biofacies associations. The first test is simply a prerequisite to further consideration of tracking, for if a majority of species do not recur or stacking order is very different from cycle to cycle, then the process of tracking is clearly refuted. The second and third tests are more stringent because they test for patterns of recurrence in three and four dimensions, respectively; that is, comparison of vertical and lateral gradients of species composition along single and across multiple time planes. The fourth test evaluates tracking quantitatively by testing for similarity of pattern coupled with offset of quantitative coenocorrelation curves. The final test assesses whether groups of facies-restricted, and ideally endemic, species always or frequently occur together. If they are endemic, they cannot be restocked from other provinces, and if they are only ever seen in particular biofacies, then they indicate the persistence of a narrow range of conditions for the duration of their occurrence; this evidence further indicates that these organisms track this narrow environmental

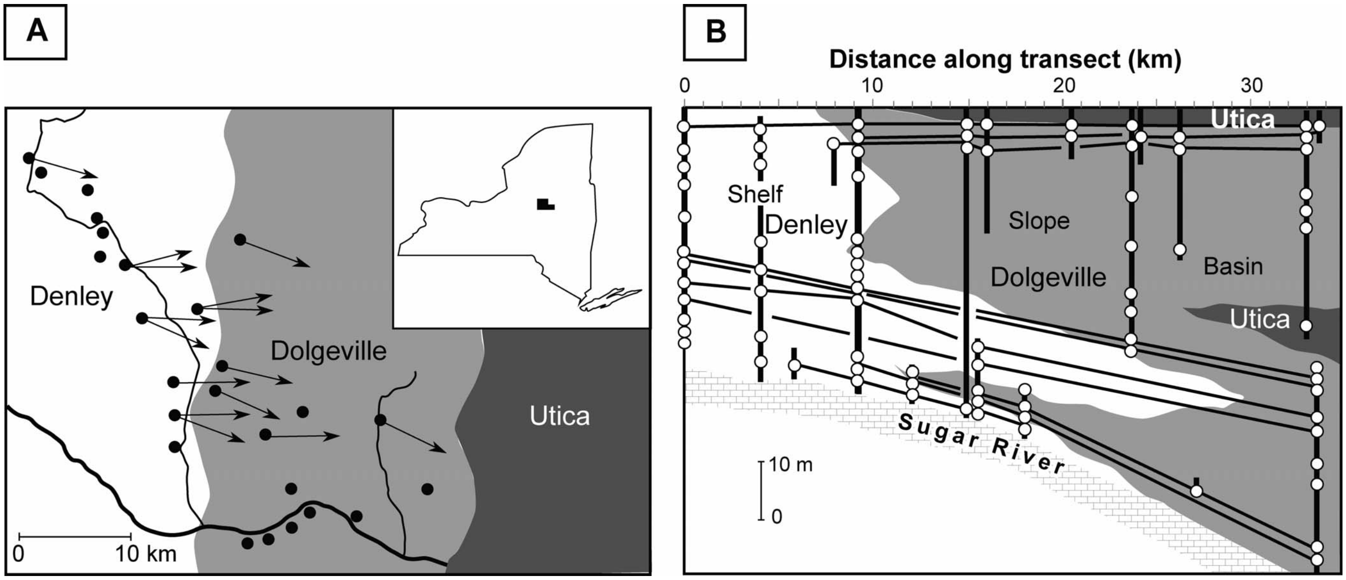

FIGURE 2—Study site for gradient analysis of Upper Ordovician Trenton Group marine biotas in the Mohawk Valley of New York State. A) Map view showing general lithofacies belts; white = carbonate platform facies (Denley Limestone: middle Trenton Group nodular wackestones to packstones); light gray = deep shelf-ramp facies (Dolgeville calciturbidite); dark gray = black, calcareous shale facies (Utica or Flat Creek Shale); arrows show paleocurrent directions based largely on graptolite orientations. B) Regional cross section of upper middle Trenton Group showing two shallowing-deepening cycles. Note positions of correlated K-bentonites used to establish isochronous transects (solid lines). Adapted and redrawn from Cisne and Rabe (1978).

window as it shifts geographically. We suggest that these approaches to assessing tracking form an important future agenda for paleoecologists.

Recurrent Replacement Series

A high proportion of recurrent species in particular associations and in similar order in sedimentary cycles suggests that species track shifting habitats and that general biotic gradients can persist for geologically long periods of time. Conversely, stacking patterns in replacement that differ strongly from one another may require such alternative explanations as the presence of discontinuities or stratigraphic incompleteness. Assuming that such artifacts can be ruled out, the order of appearance of species and biofacies in vertical shallowing or deepening successions should reflect a signature of biotic response to environmental changes (Fig. 1). If a conformable vertical replacement series appears chaotic, then a random disassembly-reassembly model may be favored instead. In addition, if gradients from comparable parts of different cycles show internal order, but differ substantially from one another in species or generic biotic composition or stacking order, then this would further indicate that biotic gradients are not relatively constant through time. An effort must be made to compare the most similar facies suites in cycles of different ages because, as noted in the following sections (and see Brett at al., 2007), organisms may respond to more than one type of environmental influence that will fluctuate in addition to bathymetrically related parameters. The observation of similar biofacies stacking patterns in cycles of different ages, thus, provides necessary but not sufficient evidence to support a model of habitat tracking. For example, disassembly-reassembly may also produce deterministic patterns of replacement.

Lateral Displacement of Biofacies along Isochronous Horizons

A second test of tracking involves direct application of the predictions of Walther's Law. Simply stated, it should be possible, within a single transgressive-regressive cycle, to demonstrate that the lateral progression of biofacies (or quantitative gradient scores) along single time planes mirrors the replacement series seen in vertical stratigraphic sections of that cycle. Such isochronous planes may be marker beds, including K-bentonites (see Cisne and Rabe, 1978; Figs. 2–3), cycle turnover points, or flooding surfaces. Within a sequence stratigraphic framework, facies gradients can be established at least for particular correlated systems tracts, and these generalized transects permit examination of approximately synchronous lateral faunal gradients. In other words, when a particular species or biofacies is absent in one portion of the basin—for example, because local conditions are too shallow—that species or association may be found in coeval strata elsewhere, in this case, shifted more basinward. If the biofacies cannot be found to exist anywhere within the basin at certain time planes, then their recurrence at various levels must be attributed to deterministic reassembly of similar associations from metapopulation pools, rather than tracking. A practical difficulty in applying this test is finding sedimentary basins with accessibility of sections both along and across depositional strike. Again, the basic Waltherian prediction of tracking is testable within the context of a single depositional cycle. Lafferty et al. (1994) and Brett et al. (2007, fig. 7) discuss examples of this approach involving cycles in the Middle Devonian Hamilton Group.

Recurrence of Lateral Biotic Gradients

Perhaps the best test for consistency of faunal gradients through time is possible where such multiple isochronous markers as correlated K-bentonite beds exist in a basin. High-resolution correlations may provide a time series of snapshots of bathymetric gradients. If the biotic gradients appear similar but shifted geographically through time, a case can be made for faunal tracking, as opposed to disassembly and reassembly of faunal associations. This inference is valid only if the time planes do not all reflect analogous parts of several cycles. In an outstanding example of recurring gradients, Cisne and Rabe (1978) were able to establish a series of transects along a Mid–Late Ordovician carbonate platform-to-basin trend in the classic Trenton to Utica shale succession of the Mohawk Valley, New York, using correlated K-bentonites as time markers (Figs. 3–4). Although some of the correlations were later found to be in error (e.g., Mitchell et al., 1994), the work of Cisne and Rabe (1978) and Cisne et al. (1984) established the general persistence of species composition along gradients through time by comparing successive transects (Figs. 2–3). Offsets in the geographic positions of successive faunal gradients indicate that the entire gradient could shift, presumably in response to sea-level oscillations (Fig. 3). This framework provided the

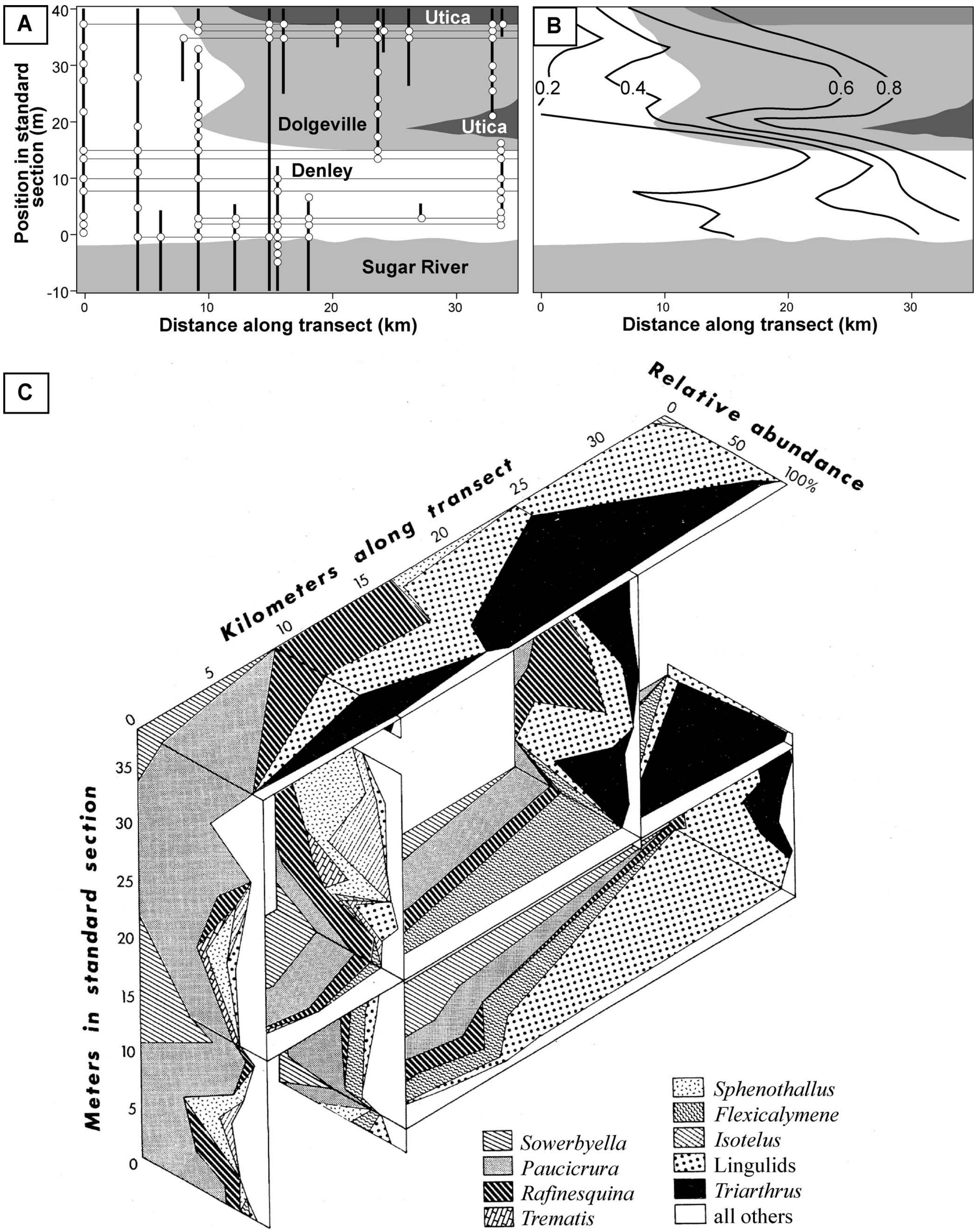

FIGURE 3—Plots of distance along west-east Mohawk Valley transect versus time (estimated as thickness in standard reference section). A) Facies change, coded as in Figure 2, showing transgressive-regressive cycles. B) Faunal replacement patterns plotting gradient analysis (reciprocal-averaging) scores versus time and distance along transects. Note approximate parallelism of trends in lines for equal scores and facies cyclicity. C) Series of three isochronous gradients along standard east-west transect, showing fluctuating relative abundance of common genera. Note general similarity of proportional abundance along successive transects, despite offset in position. The brachiopod *Rafinesquina* dominates shallow-water facies, and the trilobite *Triarthrus* typifies deeper-water (east) ends of transects. Figure adapted and redrawn from Cisne and Rabe (1978).

basis for development of the field of gradient analysis and coenocorrelation or the pattern matching of gradient analysis curves (e.g., Springer and Bambach, 1985; Patzkowsky, 1995; Holland et al., 2001; Olszewski and Patzkowsky, 2001; Holland and Patzkowsky, 2004).

Alternatively, discovery of gradients of strongly varying composition at different transects would imply variable reassociation of species and falsify a process of tracking. Obviously, this test will be applicable only in special cases in which multiple isochronous gradients exist within similar lithofacies gradations.

Correlation of Gradient Analysis Curves

A fourth indirect test of the predictions of Walther's law is closely related to the test of multiple gradient transects. Using such ordination techniques as DCA or nonmetric multidimensional scaling, it is possible to quantify gradients of species composition and to relate these to environmental gradients, especially water depth (e.g., Cisne and Rabe, 1978; Holland et al., 2001; Miller et al., 2001; Webber, 2002; Holland and Patzkowsky, 2004; Figs. 4–6). Vertical series of DCA scores based on biotic replacements in single sections can be used to generate coenocorrelation curves indicating relative environmental change. A test of tracking involves examination of coenocorrelation curves generated from a series of localities in successively more downramp or upramp positions, which are independently correlated using event beds, sequence stratigraphy, or other high-resolution methods. If groups of species track relative depth fluctuations, then the coenocorrelation curves should have the same configuration of DCA scores in correlative horizons, but the absolute values of the deeper or shallower sections should be consistently offset (Fig. 5). Lack of concordance between independently correlated curves could indicate that faunal gradients are impersistent or that species occur in local patches or random associations, but in any case would argue against tracking.

Using semiquantitative estimates of the abundance of taxa in the Late Ordovician of the Cincinnati Arch, Holland et al. (1997, 2001) and Miller et al. (2001) quantified gradients of brachiopods, trilobites, crinoids, and other groups that appear to indicate relative depth (Fig. 4). They then generated curves of DCA scores for various stratigraphic sections based on vertical sampling of fossil assemblages for various localities (Fig. 5) that form a proxy record of minor, low-amplitude, sea-level oscillation. Note that in Figure 5, the general form of the DCA curves is preserved in different localities, even though the absolute scores are shifted; this would seem to imply that the general faunal gradient is conserved and is shifted laterally through time. The degree to which such DCA curves can be correlated (coenocorrelation) serves to strengthen the argument for environmental tracking by groups of species, which share similar habitat preferences. Figure 3 shows a set of curves of equal gradient scores from the work of Cisne and Rabe (1978). Again, the various curves show similar patterns indicating shifting of gradients.

The amount of offset of scores along correlative horizons should indicate the relative depth of the sections. Indeed, this inference has recently been used to good advantage by Scarponi and Kowalewski (2004) to quantify depth differences between two sections on a Pleistocene ramp.

Environmental Fidelity of Stenotopes

Yet another line of evidence for tracking comes from the distribution patterns of stenotopic species and may be termed the test of stenotopes. Obviously, eurytopic species cannot provide a very sensitive test of tracking. If, as suggested by Miller (1990a, p. 41), "most species are represented in more than one . . . kind of ecosystem," then "populations in one local ecosystem may serve as sources for staffing in other systems." Certain species, however, are confined to very specific litho- and biofacies. This is especially true in such high-diversity faunal associations as coral-bed biotas in the Devonian of New York State, wherein more than half of the species found are confined to these associations (e.g., large rugose and tabulate corals; Baird and Brett, 1983; Brett et al., 1996; Fig. 6). The case for tracking is most strongly made for endemic stenotopes in semienclosed basins for which much of the record of the basin is preserved, as in the middle Paleozoic of the Appalachian Basin (Brett et al., 1996, 2007). Instances of incursion of species not observed in older samples of biofacies are known, and these must involve recruitment from external species pools; this process may also be involved in the recurrence of some species within biofacies. If, however, it can be argued that species could not have been restocked from other basins, and also that they are nearly always found together in associations, then it can be inferred that they must have tracked a suite of rather tightly defined environmental conditions.

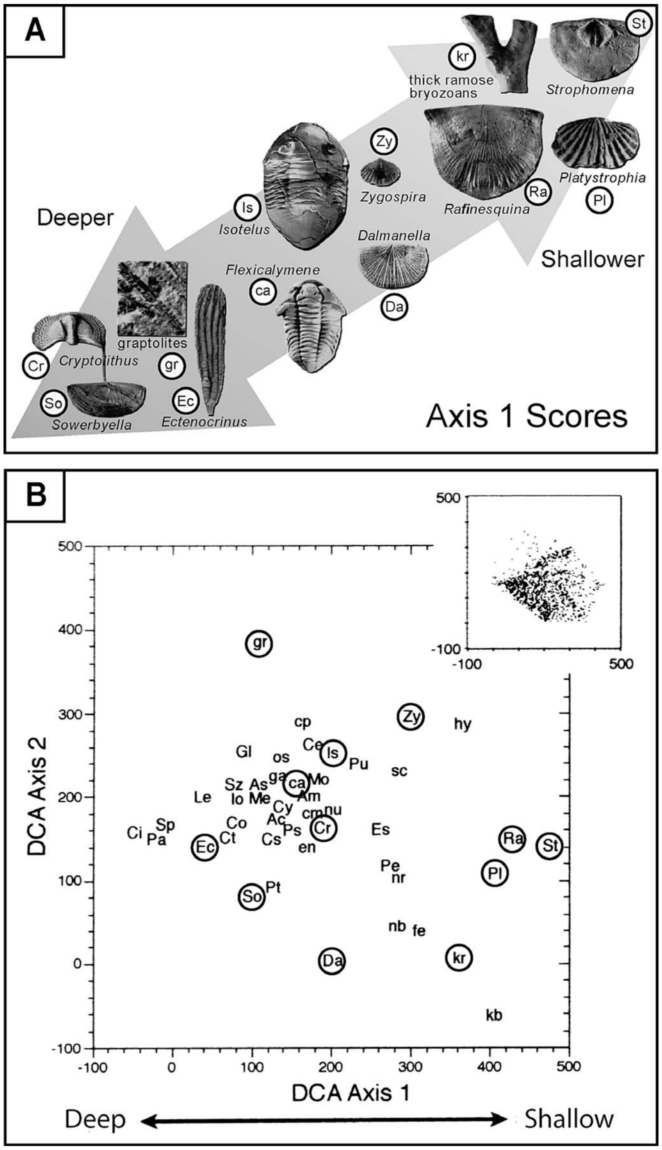

FIGURE 4—Detrended correspondence analysis (DCA) of Ordovician faunas from Kope Formation in northern Kentucky. A) Schematic diagram showing preferred positions of common genera along the depth gradient based on DCA scores for all samples. B) R-mode DCA axis 1 vs. axis 2 plot showing distribution of species along DCA axis 1 inferred to represent relative depth (inset shows Q-mode plot of all samples). A is adapted from Webber (2002); B is adapted from Holland et al. (2001).

COMPLEXITIES OF REPLACEMENT SERIES

Symmetrical and Asymmetrical Replacement Series

The vertical succession of fossils in a given section may appear nearly symmetrical, with mirror-image recurrence of assemblages around cycle

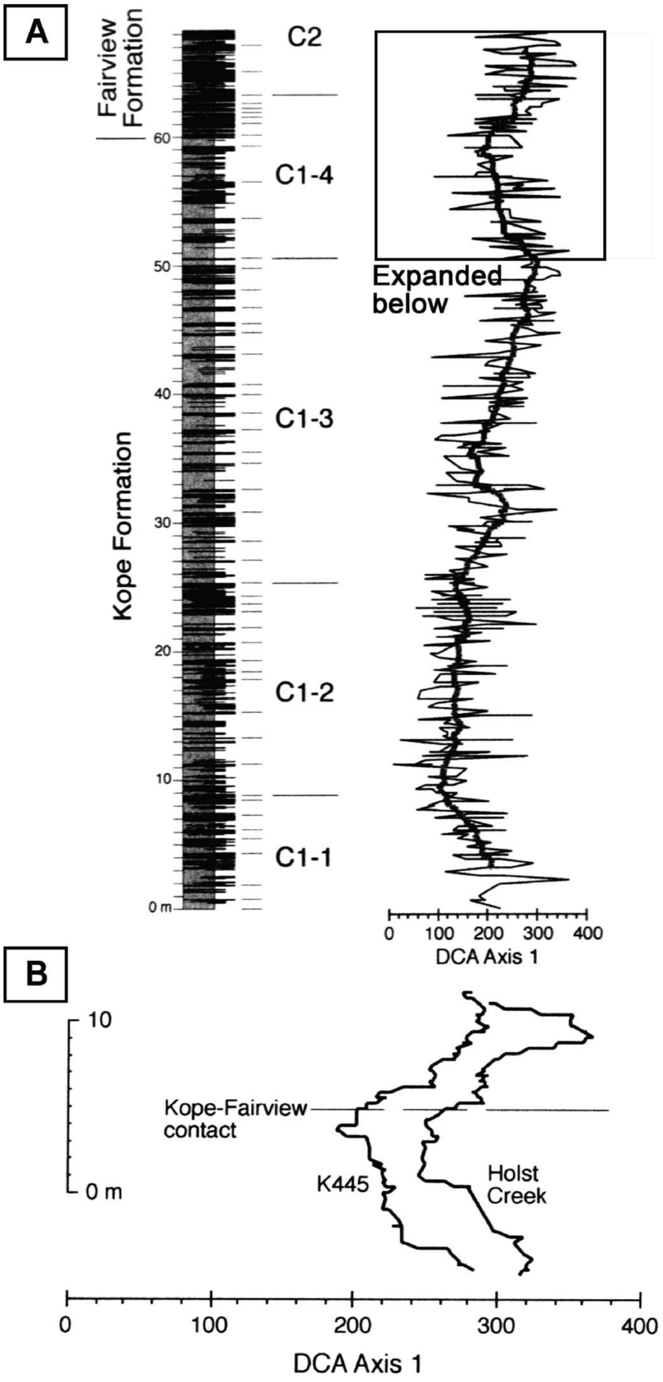

FIGURE 5—Vertical profiles showing detrended correspondence analysis (DCA) axis 1 scores plotted against stratigraphic thickness. A) Plot of DCA axis 1 scores versus thickness for middle-upper Kope and Fairview Formations at K445 standard reference section in cuts along Kentucky Route 445 and adjacent sections on Highway I-275, near Brent, Kentucky; C 1–1 through C1–4 and C-2 represent depositional sequences recognized by Holland et al. (1997). B) Expansion of upper portion of curves of 20-point moving-average scores through upper Kope and Fairview formations for two sections separated by about 80 km, showing general parallelism of curves despite offset in absolute scores. Offset in absolute scores indicates that the K445 section was consistently deeper than Holst Creek, but similarity of pattern indicates that species in each area responded to common environmental (water-depth) changes during transgressive-regressive cycles. Adapted from Holland et al. (2001).

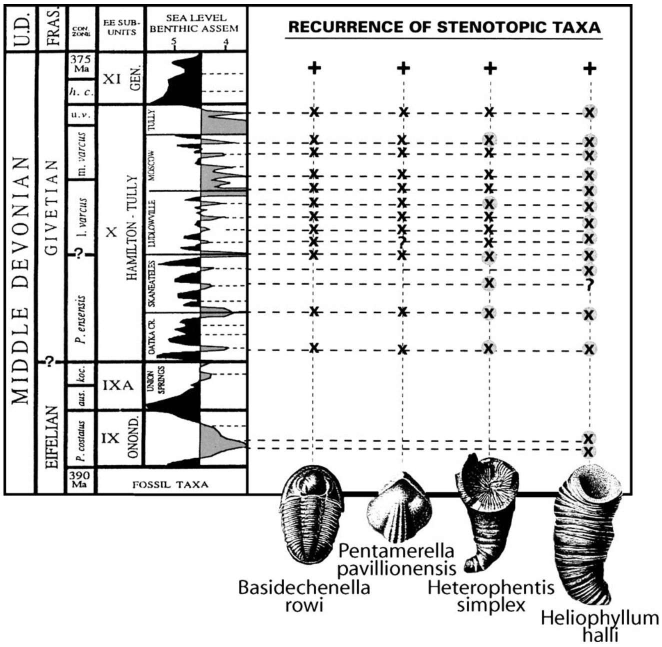

FIGURE 6—Recurrence of stenotopic species in successive fourth-order cycles of the Middle Devonian Hamilton Group and Tully Formation in western-central New York with relative sea-level curve shown to the left; numbers listed under benthic assemblage refer to depth-related benthic assemblage zones, as recognized by Boucot (1975), with BA 4 = deep storm wave base; 5 = dysoxic, below storm wave base (see Brett et al., 1990). X = the occurrence of the taxon in the shallowest, limestone-rich portion of given cycles recorded for this duration (~ 5.5 myr); gray circles around X = a common-to-dominant member of the fauna. Note that these species are not found in any of the deeper-water facies of the cycles anywhere within the basin but recur with strong fidelity in the shallowest, coral-rich facies and that these species consistently occur with each other, suggesting that they have collectively tracked a narrow range of environments. + = apparent extinction of lineages associated with a major (Taghanic) biotic turnover (Baird and Brett, 2003). Note that *Heliophyllum halli* apparently survived an earlier biotic crisis and was reintroduced into the Appalachian Basin following a period of outage during the time of fauna IXA.

centers, or markedly asymmetrical. In the case of nearly symmetrical patterns through sedimentary cycles, there is strong evidence that environments at various bathymetrically controlled positions remained nearly similar through the cycle despite lateral shifts of up to hundreds of kilometers. In particular, sedimentation rates and turbidity must have been maintained at nearly the same level even as the sea level rose and fell. In the Middle Devonian Hamilton Group of New York, a cycle typically shows an upward change from deeper, dysoxic facies with low-diversity associations dominated by leiorhynchid brachiopods in dark gray shales upward through the small brachiopod associations (*Ambocoelia*-chonetids); the latter in turn are replaced by assemblages rich in phacopid trilobites in calcareous mudstones, small rugose to high-diversity brachiopod-coral beds in argillaceous limestones, and these in turn to diverse coral, brachiopod, and bryozoan assemblages. This trend is followed upward by an approximate mirror-image spectrum of biofacies showing a transition back to dysoxic biofacies (Fig. 7; Brett et al. 1990, 2007; Sessa, 2003). Figure 7 shows this pattern quantitatively using DCA to define a gradient of species composition for the symmetrical Centerfield cycle. A plot of DCA scores versus sample-position level yields a nearly symmetrical pattern of scores (Fig. 7).

Symmetrical replacement patterns such as this are relatively uncommon. In many stratigraphic sections the vertical pattern of community replacement does not appear symmetrical through a cycle (Holterhoff, 1996; Brett, 1998). Rather, different associations occur at approximately analogous depth positions in the transgressive systems tract (TST) versus the late highstand tract (HST; Fig. 8). In many siliciclastic-influenced,

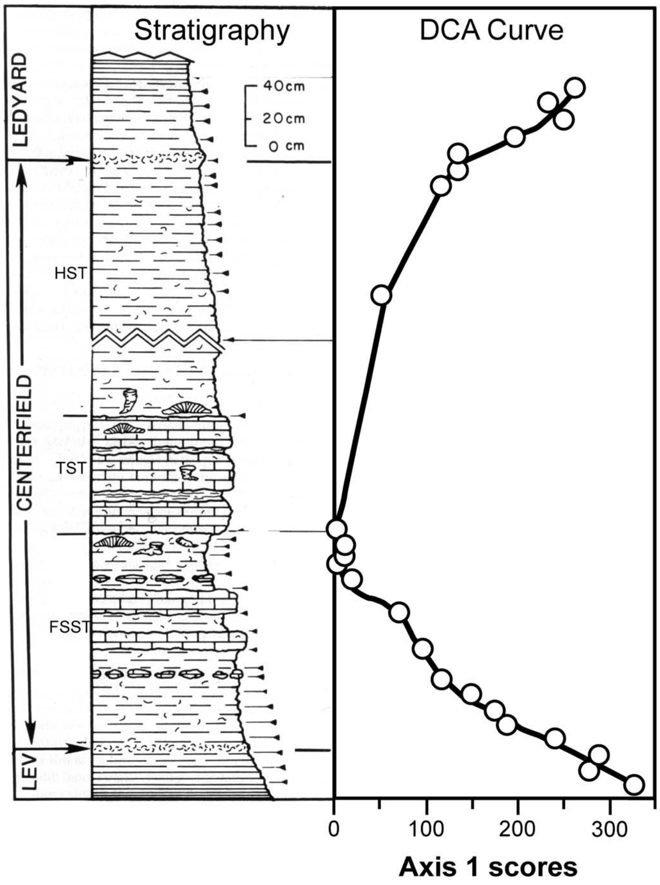

FIGURE 7—Faunal replacement and cyclicity in the Centerfield Member, Ludlowville Formation, Genesee Valley, western New York State. Detrended correspondence analysis (DCA) axis 1 scores of successive samples plotted against a composite stratigraphic section for the Centerfield Member at Browns Creek and Wheeler Gully sections, north of Geneseo, Livingston County, New York; note delineation of a nearly symmetrical cycle, suggesting an orthogonal pattern of tracking of migrating facies belts during this shallowing-deepening cycle. Compare with schematic shown in Figure 8A. LEV = Levanna Shale Member; FSST = falling stage systems tract; TST = transgressive systems tract; HST = highstand systems tract. Data from Savarese et al. (1986).

depositional environments, increased sedimentation or turbidity during relative sea-level fall favors low-diversity associations of sediment-tolerant, eurytopic taxa. Conversely, the combination of shallow, clear water and typically firm to hard media (e.g., hardgrounds, shell gravels) during sediment-starved, early transgressions makes them especially favorable to diverse stenotopic taxa, including those forming widespread shell beds, biostromes, or biohermal horizons (Kidwell, 1991; Kidwell and Bosence, 1991; Abbott and Carter, 1997; Brett, 1998). Also, note that in such cases the transgressive portion of the cycle shows greater similarity over broader areas than does the highstand or falling stage (Rollins et al., 1979, 1990; Holterhoff, 1996). Such asymmetry might appear to suggest that tracking breaks down and an alternative biofacies is reassembled from metapopulations. This may indeed be true in some instances. In other cases, however, it is evident that preexisting biofacies have not disappeared but merely become confined to areas elsewhere in the basin (Holterhoff, 1996; Brett et al., 2007). Such expansion and contraction of given biofacies during different phases of cycles, however, does not necessarily falsify tracking because the faunal associations may shift laterally along depth-zone belts as well as perpendicular to shore. Biofacies may be arrayed along more than one gradient simultaneously, for example, a depth-related gradient perpendicular to shoreline and a sedimentological gradient along a given bathymetric belt. The three-dimensional trajectory of a given biofacies, thus, can be complex, with a component of movement perpendicular to the shoreline as well as a vector perpendicular to the sediment source area (see Brett, 1998, fig. 6).

Holterhoff (1996) argued that certain associations of species were unique to the transgressive systems tracts, forming an alternative community. He noted that all of the crinoid species present in the unusual transgressive biofacies were also present at least very rarely in other biofacies. He surmised that these species survived in suboptimal metapopulations during regressions and that unique associations reassembled in the distinctive environmental conditions that characterized transgression, although he also acknowledged that the transgressive biofacies could have existed in localized areas during the less favorable conditions of the late highstands or regressions. This possibility cannot be ruled out unless a large portion of the basin is preserved and available for study.

Holterhoff's alternative community explanation rests on the fact that most taxa examined were eurytopic to a degree, and in this case reassembly of various combinations of taxa into alternative communities is plausible. Moreover, alternative-community states may be anticipated in times of such rapidly fluctuating climates as the Carboniferous when Waltherian facies shifting may break down (Soreghan, 1997).

In other cases, however, a majority of species in high-diversity biofacies (see discussion of Diverse Coral Bed Biofacies; Brett et al., 2007) appear to be restricted to a narrow range of conditions. Such stenotopic organisms, adapted to low turbidity and low sedimentation rates, proliferated during transgressions. Obviously, however, they did not entirely disappear during regressions but merely became confined to a smaller proportion of the basin where their preferred habitats persisted. Studies of depositional sequences in the Middle Devonian Hamilton Group confined to the eastern and central portions of the Appalachian foreland basin would conclude that coral-rich associations did not exist, as such, during regressive portions of cycles; direct tracing shows that such associations were, in fact, present in typical form on the western basin margin during these regressive phases. Likewise, nearly all faunal associations typical of both transgressive and regressive portions of Plio–Pleistocene cycles are known to exist contemporaneously on modern shelves of New Zealand (Hendy and Kamp, 2007). The modern shelf molluscan assemblages primarily reflect those species that are tolerant of higher siliciclastic input, as predicted by the general highstand condition of modern New Zealand shelves. Associations of species that are stenotopic to low-sedimentation environments, however, still exist in some areas that are sheltered from siliciclastic input. This pattern implies not only shore-perpendicular but also lateral migration of biotas along depositional strike (cf. Holterhoff, 1996, p. 72).

During TSTs with the predicted sequestering of siliciclastic sediments, low-sediment stenotopic organisms could flourish over a much broader area. Conversely, those organisms that tolerate or favor higher-sedimentation rates or particular (e.g., silty) sediment textures may become confined to a smaller part of their former distribution. An important inference is that low-diversity, eurytopic assemblages may be much more widespread during regressive phases of cycles, while diverse, stenotopic assemblages, including coral biostromes, may be much more widespread during transgressions. Rollins et al. (1990, p. 28) noted that bathymetrically arranged, parallel communities should be most obvious in the transgressive part of the cycle. Similarly, Scarponi and Kowalewski (2004, p. 991) note that, in Pleistocene shallow marine benthic species, "samples are highly uniform taxonomically during late TSTs and highly variable in . . . HSTs" (also see Abbott and Carter, 1997; Hendy and Kamp, 2007). We would agree that this is true in areas strongly affected by siliciclastic input. Such bathymetrically zoned communities, however, are equally well displayed during highstand and falling-stage systems tracts in areas away from the clastic sources where nearly symmetrical cycles may be developed (Savarese et al., 1986; Brett, 1998; 2007; Fig. 7, herein).

Within limits, the expansion or contraction of habitable area does not appear to seriously affect species or their associations. For example, shallow-water, high-diversity coral-brachiopod biofacies in the Middle

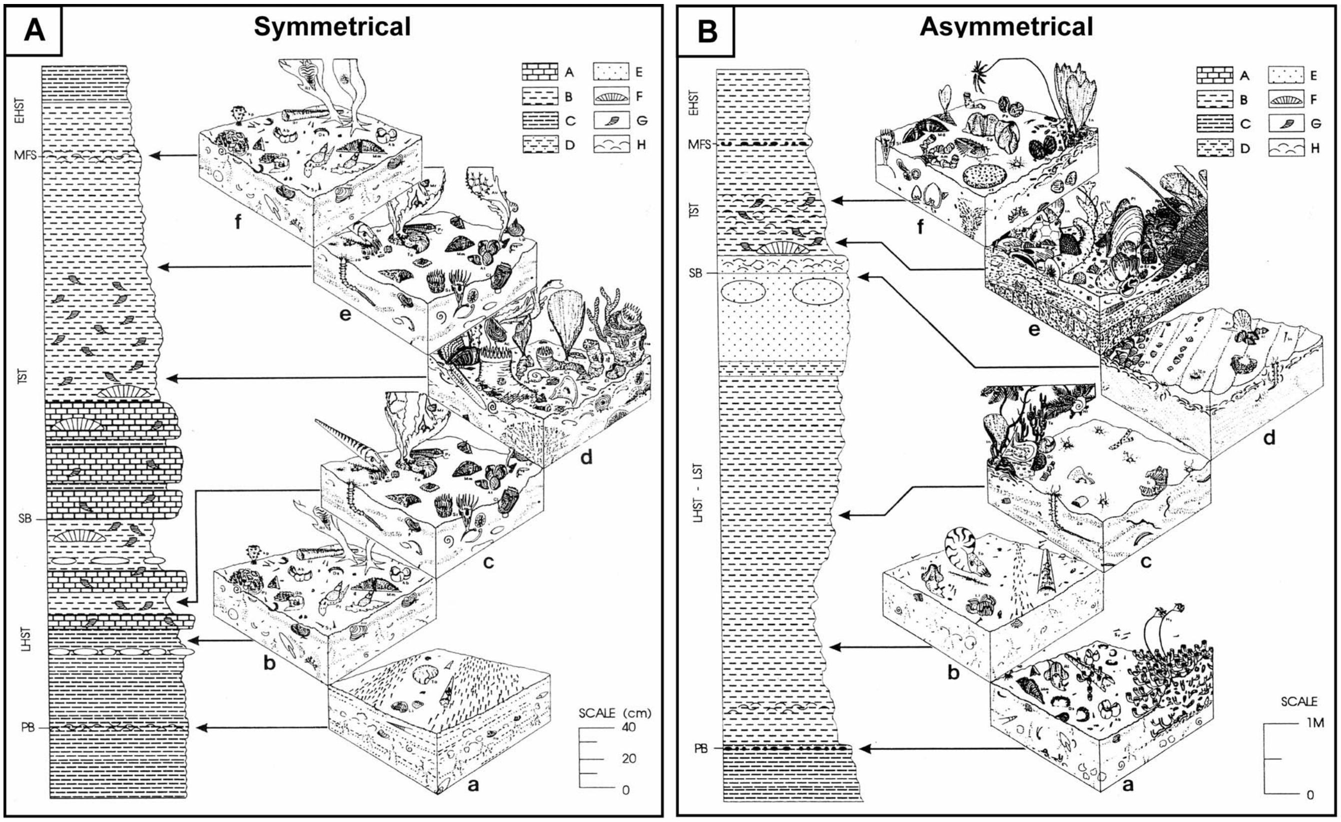

FIGURE 8—Symmetrical and asymmetrical replacement patterns within a single cycle in (A) western and (B) west-central New York State. Note distinct difference in faunas of correlative lower shallowing-upward cycle between the two areas and similarity of pattern in the transgressive (upper) portion of cycle throughout the region. Lithological symbols: A = skeletal limestone; B = grey mudstone; C = dark platy shale; D = calcareous shale; E = quartz arenites; F = favositid coral; G = rugose coral; H = brachiopod shell bed. Biofacies codes (a–f) are defined in Brett (1998), from which this figure has been adapted. Abbreviations for sequence stratigraphic terminology: TST = transgressive systems tracts; EHST = highstand systems tracts; LHST = late highstand systems tracts; SB = sequence boundary; MFS = maximum flooding surface; PB = precursor bed.

Devonian Hamilton Group show approximately a fourfold reduction in outcrop area of occurrence during regressions relative to earlier transgressions (Brett et al., 2007); however, these areas are still probably many thousands of square kilometers in size and provided ample areas for survival of nearly all species. This fractionation of the high-sedimentation and low-sedimentation faunal assemblages into TSTs and HSTs, respectively, has a broader implication for tracking. Species do not respond to a single factor, such as depth fluctuations, but to a complex combination of variables. Moreover, not all species were responding to precisely the same combination of variables (Jackson and Overpeck, 2000).

Interactions of Succession and Replacement Series: Fine-Scale Noise

An important aspect of replacement series is a pattern of high-frequency variation in specific composition that emerges when many successions are sampled at a scale of individual beds. For example, Figure 5A (modified from Holland et al., 2001) shows a degree of high-frequency variation in DCA scores that is equal in magnitude to the major stratigraphic trends that tracking can explain quite well. The samples in this study were relatively small, which undoubtedly increases the variance of ordination scores, but such noise is present even in ordinations with larger samples (Bennington and Bambach, 1996). This phenomenon probably arises because of preservation of snapshots of patchy benthic communities that developed over various periods of time following disturbance of the seafloor and episodic pulses of rapid sedimentation that prevent the smoothing effects of time-averaging (cf. Johnson, 1972). As already noted, short-term successions may partially mirror replacement series in that early pioneering colonizers are dominated by opportunistic, eurytopic species that also dominate in such stressed environments as dysoxic or turbid deeper parts of stratified basins. The superposition of episodic disturbance events, especially blanketing of seafloors by muds, on a longer-term signal of environmental change (e.g., shallowing or deepening) may well produce the high-frequency noise seen in these studies. Episodic disturbance may produce significant local, short-term disruption. Indeed, evidence from widespread obrution deposits, traceable for up to a few hundred square kilometers (Brett et al., 1986; Brett and Taylor, 1997) indicates that seafloor biotas could be locally or even regionally annihilated, and, yet, overlying beds show no reduction in numbers of the species involved. Recolonization probably involved settlement by juveniles or larvae recruited from nearby nondisrupted areas of larvae in the water column. Thus, at a fine scale, disruption and reassembly of benthic populations and associations must take place, as per metapopulation models. This fine-scale pattern does not argue against tracking but may show how the pattern operates at a fine scale.

The pattern in Figure 7 appears much more consistent with faunal tracking and presents a strong contrast to the previous example. The reasons for this are not entirely clear, but this Middle Devonian section is probably more condensed than the Ordovician Kope Shale example; time-averaging may have smoothed out the high-frequency signals, as has been done in the moving point average curves in Figure 5. Similarly, Webber (2003) demonstrated a significantly greater consistency of DCA scores in time-averaged limestone beds than in shales of the Kope Formation.

Variation in the Relative Abundance and Taxonomic Composition of Biofacies

Despite sometimes marked similarities, no two recurring biofacies samples are ever identical (e.g., Bennington and Bambach, 1996). Presumably, this is because bathymetrically and sedimentologically analogous environments are never exactly constant in other physical-chemical aspects (e.g., hydraulic regime, sediment consistency, nutrient availability) through time and because species respond independently to a variety of parameters, many of which are not obviously recorded in sediments.

Subtle variation in the taxonomic composition of recurrent biofacies through time is inevitable. For example, *Pseudoatrypa*, normally a common-to-dominant taxon in diverse brachiopod biofacies, becomes uncommon to very rare in certain cycles in the Middle Devonian Hamilton Group (Brett et al., 1990). These taxa clearly show an individualistic response to an as yet unknown environmental perturbation (e.g., a species-specific pathogen). The remainder of the fauna is quite similar to that of analogous biofacies in other cycles. Neither such outages nor epiboles of normally rare species appear to cause major restructuring of the remainder of biofacies.

In addition, detailed studies involving quantitative abundance data have shown that, even in cases in which taxonomic composition is very similar between samples of different age, the rank and relative abundance of taxa may show significant differences. This is well exemplified in studies of Pennsylvanian marine faunas in the Appalachian Basin (Bennington and Bambach, 1996) and in small brachiopod assemblages (Bonuso et al., 2002b) and recurrent coral-brachiopod-rich beds (Bonelli et al., 2006) in the Middle Devonian Hamilton Group. Fürsich and Aberhan (1990) found that rank abundance of abundant species in Jurassic level-bottom assemblages was relatively stable through time, but less common forms showed fluctuations.

Differences in rank abundance of various species in compositionally similar assemblages may represent slight differences in conditions not recognizable in the sedimentary record (e.g., temperature, water chemistry). These environmental changes are not sufficient to break down gradients or eliminate stenotopes but may still shift the balance in favor of one species or another. Alternatively, shifts in rank abundance could indicate random differences related to dispersal (i.e., because species track independently); species may, by chance or by better dispersal, become established first and then become more abundant than before (Bennington and Bambach, 1996).

DISCUSSION

Variable Patterns of Recurrence and Replacement of Biofacies

Multiple lines of evidence indicate that biofacies can recur with considerable fidelity during all phases of depositional cycles. This further suggests that biofacies tracking, at least in shallowly dipping shelf and ramp settings, is a real and perhaps widespread phenomenon. This is not to say that other such patterns as disassembly and reassembly may not apply in many other situations. Furthermore, at a fine scale, deterministic reassembly, for example, after local decimation of populations along extensive biofacies belts, may be a part of tracking; the key point is that general biofacies gradients do not break down.

Several questions arise with respect to the notion of replacement that are considered in reviewing several recent studies: (1) how similar are recurrent biofacies, and (2) how similar is their order of recurrence along gradients or in vertical stratigraphic cycles? The first question needs to be considered in terms of a hierarchical approach as advocated by Allen and Starr (1982) and Rahel (1990). Samples of comparable biofacies can be compared, in order of successively stronger degrees of stability, in terms of species richness, guild structure, species or generic membership, or relative and rank abundance.

Detailed quantitative studies of recurring biofacies have reported varying levels of similarity and at a variety of scales (Table 2). Many of these studies, which have been undertaken on varied scales, have come to markedly different conclusions with regard to compositional and relative abundance similarity of species assemblages from purportedly analogous environments. On the one hand, studies like that of Buzas and Culver (1994) and Stanton and Dodd (1997) suggest that species- and even genus-level composition of analogous biofacies are ephemeral (but see Buzas and Culver, 1998), that communities are highly dynamic in terms of membership, and that gradients do not persist. Other studies have demonstrated at least some degree of persistence in guild structure, richness, and composition at the genus level (Olszewski and Patzkowsky, 2001; Holland and Patzkowsky, 2004). Still others find similarities in richness and composition at a species level, with minor to substantial variation in relative and rank abundance (Fürsich and Aberhan, 1990; Brett and Baird, 1995; Bennington and Bambach, 1996; Pandolfi, 1996; Scarponi and Kowalewski, 2004; Visaggi, 2004; Bonelli et al., 2006; Brett et al., 2007).

Differences in conclusions among these studies probably reveal a mixture of real and apparent effects. Such settings as the highly mosaic, localized environments of the California Salton Trough may favor rapid species turnover and rather random and fluctuating composition of biofacies through time (Stanton and Dodd, 1997). In contrast, broad shore-parallel belts of biofacies along epeiric ramps may have favored much more taxonomic stability and long persistence of at least generic, if not species, associations and gradients (Table 2). Certain times of generally stable conditions, albeit with sea-level oscillations, may have promoted stability in biotic composition and tracking, while times of more variable or higher-intensity changes may have favored a much more random and rapid pattern of biofacies change.

In at least some cases, however, the observed differences may be a sign of incomplete sampling. It is unlikely that strong recurrence will be observed through all cycles at a single locality or limited geographic area. Progradational shallowing and changing patterns of subsidence or epeirogenic uplift and sediment depocenters through time may limit access to particular depth-related facies through time. Furthermore, even if the same array of bathymetric settings is recorded in a given area, long-term changes in sedimentation patterns and depocenters may result in preservation of very different environments through time.

It should be noted that, even if a basin is incompletely known, the occurrence of samples of very similar biofacies at multiple levels within the limited framework supports an interpretation of tracking. Conversely, claims for nonrecurrence of biofacies (e.g., Bonuso et al., 2002a) can be considered valid only if a large portion of a depositional basin is available and has been examined, as the appearance of dissimilarity among samples of different age may reflect chance interception of different portions of environmental gradients. Equivalence can be established by limiting comparisons to samples of differing age with shared taxa (Olszewski and Patzkowsky, 2001; see also Brett et al., 2007).

Significance of Tracking for Evolutionary and Ecological Stasis

The phenomenon of long-term morphologic stasis (taxonomic stasis), as well as relative stability of faunal-floral associations (ecological stasis), may be related to the ability of species to track or migrate with preferred environments. The term coordinated stasis (see Brett and Baird, 1995; see also DiMichele, 1994; Baumiller, 1996; Brett et al., 1996; Ivany, 1996; Miller, 1997; Patzkowsky and Holland, 1997; Buzas and Culver, 1998) was intended to denote a pattern of approximately concurrent long-term stability and abrupt change in many taxa. During a large proportion of geologic time, a majority of species shows little or no net change in morphology (see the review in Eldredge et al., 2005). The concept of coordinated stasis further suggests that these periods of stasis may be concurrent for many different species. Moreover, associations of species or biofacies also may be similar throughout blocks of stability referred to as ecological-evolutionary units and ecological-evolutionary subunits.

Taxonomic stasis may be partially explained by the ability of species (individualistically) to track preferred environments. Provided that populations can survive simply by shifting their distribution patterns, they may have little tendency to adapt to change. As Eldredge (1995) has put it, evolution may be the solution of last choice. Conversely, the mixing of metapopulations during environmental change may also act to undo any anagenetic changes that accumulate owing to natural selection in

TABLE 2—Summary of recent publications dealing with faunal replacement and tracking. The fourth column indicates the temporal duration of the total study interval (upper number) and of each cyclic increment (lower number); the last four columns indicate whether a strong degree of similarity was found in comparison of temporally separated, analogous biofacies in terms of (1) richness, that is, the number of species (spp.) or genera (gen.) considered in the study and whether they were found to be relatively constant (>60% persist) or variable through the study interval; (2) guild structure; (3) taxonomic composition (Comp.) at a species or genus level; and (4) relative or rank abundance (Abund.).

Age and Location	Taxa and environment	Publication	Interval-Duration	Richness	Guild struct.	Comp. species genera	Abund. Relative-Rank
Pleistocene: 1 TR cycle; Po Plains, Italy	mollusks shallow shelf	Scarponi and Kowalewski, 2004	125 kyr	132 spp. ∼constant	yes	yes yes	yes
Pleistocene: two reefs, Bahamas	gastropods	Gardiner, 2001	4–5 kyr 1.5 kyr	54 spp. ∼constant	yes	yes yes	?
Pleistocene: reefs; Papua, New Guinea	corals reef crest shoal	Pandolfi, 1996	95 kyr 95 kyr	109 spp. ∼constant	yes	yes yes	no
Pliocene, shallow marine shell beds in Pecten Zone Kettleman Hills, California	varied invertebrates local basins	Stanton and Dodd, 1997	4 myr 400 kyr	∼50 spp. variable	yes	no no	no
Tertiary: 55 My Atlantic Coastal Plain	foraminifers shallow shelf	Buzas and Culver, 1994	55 myr 1.5–24 My	356 spp. variable	?	no yes	no
Oligocene: 3 100-kyr cycles Coastal Plain, Alabama	mollusks shelf	Visaggi, 2004	∼300 kyr ∼100 kyr	94 spp. ∼constant	yes	yes yes	no
Mid-Late Jurassic: 6 depositional sequences Western Interior, USA	mollusks foreland basin	Tang and Bottjer, 1996	20 myr several myr	4–41 spp. variable	yes	yes yes	?
Pennsylvanian: 5 major cyclothems Midcontinent, USA	crinoids, epeiric sea	Holterhoff, 1996	1.2 myr 400 kyr	∼30 gen. approx. similar	yes	yes? yes	?
Pennsylvanian-Permian: 52 cyclothems; 4 major cycles Mid-continent, USA	brachiopods, mollusks epeiric sea	Olszewski and Patzkowsky, 2001	2.5 myr 50 kyr	40 gen. variable	yes	no? yes	no
Late Ordovican: 2 3rd-order sequences Cincinnati Arch, Kentucky	brachiopods, mollusk	Holland and Patzkowsky, 2004	2.0 myr 400 kyr	40 taxa variable	yes	no yes	no
Middle-Late Cambrian 1 grand cycle Great Basin, USA	trilobites shallow shelf	Westrop, 1996	∼5 myr 0.1–1.0 myr	∼40 gen. variable		no	no

isolated populations, yielding net stasis (Eldredge et al., 2005). In fact, the development of subtle anagenetic trends within particular biofacies, as documented in brachiopods by Lieberman et al. (1995), may indicate relative stability of biofacies through time, despite their lateral translation in space, as predicted in the *plus ça change* model of Sheldon (1996), in which anagenetic evolution is argued to be more likely in stable than in fluctuating environments.

In turn, ecological stasis, to the extent it exists, appears to be linked to tracking (Ivany, 1996). The retention of habitat preferences by species is a most important aspect of ecological stasis, and it has been eclipsed by arguments about the integrity of communities. In some ecosystems, consistent groups of species tend to occur together and form recurring biofacies primarily because most species maintain a set of similar and broadly overlapping physical tolerances.

Viewed in this perspective, the variable results of many recent ecological-evolutionary studies, some showing long-term stability and others showing more nearly continuous changes (Table 2), should come as no surprise. As emphasized by Jackson and Overpeck (2000), not all ecosystems behave in the same way. The highly variable environmental mosaics of continental environments thus rarely show evidence of biofacies tracking; the same may be true of some marine environments. Although some of these results may reflect an artifact of incomplete data and a failure to compare analogous samples, many may represent genuine differences in conditions at various times and places. Tracking of biofacies belts may be largely a feature of broad, gently dipping shelves and ramps and thus should not be expected in such mosaic environments as the California borderland basins studied by Stanton and Dodd (1997). Biofacies gradients do appear to be resilient to major sea-level changes, and therefore similar biofacies may recur following major sea-level changes that, for example, produce sequence boundaries (as in the Hamilton example). Tracking of assemblages, however, will be observed only where most conditions are maintained within a narrow range with only a few parameters (e.g., relative sea level) changing gradually. As noted by Ricklefs (1990), apparent ecological stasis suggests persistence of environments for evolutionary time scales. Even in such cases, the specific sites of particular parts of faunal gradients can be displaced laterally and altered considerably as a result of variations in other parameters. If climate, salinity, or other parameters are highly variable, then species compositions will be comparably variable (e.g., Aberhan, 1993, 1994).

A common response of marine benthic species to sea-level change and other normal environmental disruptions is not evolution, extinction, or large-scale emigration but, rather, local migration (Jackson and Overpeck, 2000). Major disruptions, extinction, evolution, and immigration may also be precipitated by sea-level change, but probably only when that change is accompanied by regional loss of habitat being tracked. Under appropriate conditions, however, most species and biofacies in a local ecosystem can persist for intervals several times as long as the Pleistocene Epoch.

CONCLUSIONS

In this paper we review and discriminate among patterns of biotic change in shallow marine biotas at varying temporal scales from ecological succession to intermediate-long term replacement and biotic turnover. We define and contrast the process of habitat tracking at species and biofacies level with nontracking modes of replacement. We then develop a series of tests for tracking at the biofacies level, based largely on Waltherian principles. Habitat tracking at a biofacies level is a special case of semi-independent tracking by species; tracking by biofacies is favored by gradual variation in a few such parameters or composite factors, such as water depth. It may be important in cases of gradually sloping ramps and shelves in which biofacies are arrayed in long shore-parallel belts, as is demonstrably true for many epicontinental sea and foreland-basin settings.

To summarize, consider again the questions posed at the outset and their implications for larger issues in evolutionary paleoecology. Is tracking real at a species level? Yes, evidence of persistence of stenotopic, endemic taxa indicates that species track specific environments with considerable fidelity. In many cases it is not necessary to postulate external reservoirs and continual restaffing of local communities from outside sources. Consideration of endemic stenotopic species and associations certainly suggests that locally shifting biofacies belts are the primary reservoirs.

Do biofacies track? A high degree of recurrence of species in particular marine shelf associations and in similar order in sedimentary cycles of different age suggests strongly that general biotic gradients can persist over periods of several million years. In some cases, particular biofacies maintain very similar species richness and guild structure through time. Habitat tracking applied at the level of biofacies, however, is not a group phenomenon. Most species appear to have independently tracked their preferred environmental parameters. It is likely that the recurrence of biofacies with similar species lists represents similar ranges of tolerance of many species and, therefore, similar responses to environmental fluctuations, not tight ecological structure (*contra* Sterelny, 2001).

What degree of ecological similarity is observed in recurrent assemblages? Most species appear to maintain similar ranges of habitat tolerance (especially bathymetric ranges) through time; this applies to rare as well as common species (cf. McKinney, 1997). Certainly in many cases the basic guild structure, in terms of proportions of various trophic and life habit groups, may recur with great similarity in particular biofacies (e.g., Bennington and Bambach, 1996; Brett et al., 2007). Moreover, overall values of richness may recur (or be maintained) to within just a few species more or less in recurrent samples. Hence, the physical tolerance ranges do persist within most species, although different species of the same genus may show markedly different habitat preferences and tolerances.

Are relative and rank abundance of species maintained in recurring associations? No, a majority of studies do not observe persistence of precise rank and abundance structure. Just as no two samples of a given lithofacies are ever exactly the same, so no two recurrent biofacies are identical (Bambach and Bennington, 1996; Bonuso et al., 2002a, 2002b; Bonelli et al. 2006). This result has important implications for evolutionary ecology, as it indicates that species do not form tightly integrated stable entities (*contra* Morris et al., 1995). Biofacies may track shifting environments, not because they form cohesive units, but primarily because individual species have closely overlapping environmental tolerances (cf. Buzas and Culver, 1998).

Important issues for future research include (1) development of more thorough, rigorous tests for tracking of biofacies, and (2) further exploration of nontracking modes of species replacement and comparative studies to further determine settings that favor tracking versus various assortive reassociation processes. Last, the relationship of modes of replacement to evolutionary stability needs further attention. Tracking of biofacies, when it does occur, may be important in maintaining patterns of concurrent stasis, and the converse also may be true.

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