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COMMUNITY REPLACEMENT IN ESTUARINE PLEISTOCENE DEPOSITS OF EASTERN NORTH CAROLINA

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I. ABSTRACT

Nearly all examples of succession described from studies of fossiliferous sequences are, in fact, instances of a wholly different synecologic process. This process is *community replacement*, the gradual to abrupt substitution of one benthic community for another during changes in environmental settings. Requiring time spans intermediate between those needed for succession and community evolution, replacement yields a fossil record that can be termed a *community replacement sequence*. Such subevolutionary sequences arise by 1) gradual replacement, mainly involving adjustments in species-abundance distributions with some minor species turnover, caused by slight alterations in habitats; and 2) attritional replacement, dominated by species turnover in habitats subjected to more rapid and drastic environmental change.

A sequence of fossil beds in the middle Pleistocene Flanner Beach Formation, Neuse River valley, North Carolina, represents a case of gradual community replacement. The community replacement sequence is reflected in the following vertical order of estuarine fossil associations within the Smith Gut and Beard Creek members: (1) open bay; (2) slightly restricted bay; (3) restricted lagoonal; (4) open lagoonal; and (5) lagoonal firm-ground. The proximal causes of replacement of the Flanner Beach communities were long-term changes in average salinity levels and intensity of seasonal environmental rigor, and, to a lesser extent, changes in substrate properties. These were ultimately related to a changing geomorphic configuration as barrier islands formed and isolated this segment of the western Atlantic coastline during an interglacial high-stand of sea level.

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II. INTRODUCTION

This paper surveys community temporal dynamics, emphasizing the importance and uniqueness of replacement in the temporal-ecologic hierarchy of community changes. These changes range from authentic ecologic succession to community evolution, and involve biologic interactions, purely environmentally driven changes, or both kinds of forcing mechanisms acting together (Miller, 1986). A case of gradual community replacement preserved as a sequence of estuarine fossil associations is documented from the middle Pleistocene Flanner Beach Formation in the Coastal Plain of eastern North Carolina (Figure 1), and an attempt is made to identify the kinds of long-period changes in environmental factors that influenced the Flanner Beach soft-bottom communities. Finally, a conceptual model of gradual replacement of benthic communities, based on the Flanner Beach case study, is described.

III. COMMUNITY TEMPORAL DYNAMICS – A PALEOBIOLOGIC PERSPECTIVE

Temporal change in composition and structure of communities has been a dominant theme of ecological research since the first scientifically cogent treatments of succession-like phenomena were published early in this century (*e.g.*, Cowles, 1901; Clements, 1916). However, paleontologists did not develop an interest in similar themes until the appearance of Lowenstam's (1950, 1957) classic papers on ecologic zonation and development of Silurian reefs.

Paleoecologists have often confused or misinterpreted one or more of three major aspects of community temporal dynamics: (1) the temporal scope of processes that yield preservable patterns in the fossil record; (2) whether dominant control was autogenic or allogenic; and (3) the number of different communities involved in resultant patterns. Ecologists also have shown con-

TABLE 1. Patterns and rough estimates of durations of the different types of temporal dynamics involving soft-bottom marine and estuarine communities.

Process	Pattern	Approximate Duration (Years)	Predominant Interaction Involved
COMMUNITY EVOLUTION	Origin and development of new community types, community structural divergence, community displacements and major faunal turnovers; yields *community lineages*	10^5–10^7	Species-Environment, Species-Species
COMMUNITY REPLACEMENT	Abrupt to gradual community transitions caused by environmental changes yielding *community sequences*	10–10^5 (?)	Population-Environment
PATCH DEVELOPMENT	Amalgamated seres and/or pseudoseres	10–10^3 (?)	Organism-Organism and/or Organism-Environment
COMMUNITY RESPONSE	Allogenic, seasonal or cyclic response to short-period environmental changes yielding *pseudoseres*	1–10 (?)	Organism-Environment
ECOLOGIC SUCCESSION *(sensu stricto)*	Autogenic, biotic changes in community structure yielding *seres*	1-10	Organism-Organism

fusion with regard to the last two of these properties (see discussion in McCall and Tevesz, 1983). Many recent paleoecologic studies describe changes within vertical sequences of fossils as some form of succession, operating through a wide range of time spans, and driven by both dynamic biologic processes within communities and by changes in environmental gradients or qualities. McCall and Tevesz (1983, p. 159), in discussing the concept of "allogenic succession," criticized the practice of mixing temporal hierarchies, invoking both autogenic and allogenic causative factors, and generally misapplying the concept of succession in stating: "It is against the weight of the more common usage of the term *succession*, it is confusing, and it is overbroad, emptying the idea of succession of any nontrivial meaning." They argued for restriction of the term succession to changes occurring in communities during short periods of time (usually less than ten years for soft-bottom communities) caused for the most part by internal, biotic interactions shaping composition and structure. More rigorous application of concepts in the recognition, description, and modeling of temporal dynamics would eliminate much of the existing confusion and facilitate better communication with ecologists.

To show the differences between patterns of change through time in benthic communities, major categories of temporal dynamics are briefly outlined, beginning with changes that are framed in the shortest durations (Miller, 1986). Table 1 is a summary of this hierarchy of community changes.

Ecologic Succession. Because of persistent interest in successional patterns and processes, a vast literature has accumulated on these subjects, mainly with regard to terrestrial plant communities (for good reviews see: Keever, 1950; Odum, 1969; Drury and Nisbet, 1973; Horn, 1974; Pickett, 1976; Connell and Slatyer, 1977). Definitions of ecologic succession usually contain three elements: (1) Succession is a change in the composition and structure of a community through time, following the invasion of an unoccupied habitat. (2) Changes in composition and structure result primarily from population interactions within the successional system. (3) Succession is "orderly" in the sense that patterns (seres) can be more or less recurrent in space and time, and because the life-history strategies of component populations and complexity of biotic interactions change regularly during successional sequences (McCall and Tevesz, 1983; Odum, 1969, Table 1). I exclude from this category of community change so-called "allogenic succession," encompassing short-period, environmentally-controlled temporal dynamics, as well as longer-period, subevolutionary transitions, such as community replacement as defined below.

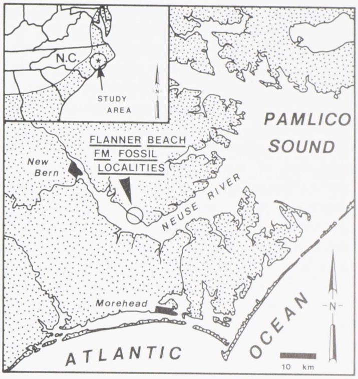

Figure 1. Location map showing fossil localities in the Flanner Beach Formation, eastern North Carolina. Stippled pattern represents extent of Atlantic Coastal Plain deposits.

Studies of modern estuarine soft-bottom succession that are relevant to interpretation of sequences of autochthonous fossil associations include: Boesch *et al.*, 1976; Levinton, 1977; McCall, 1977; Rhoads, Aller, and Goldhaber, 1977; Rhoads, McCall, and Yingst, 1978; Rhoads and Boyer, 1982; and McCall and Tevesz, 1983. These contributions point out three important properties of benthic community succession in modern environments: (1) successional sequences take place in timespans about as long as the lifespan of the most long-lived, slow-growing species, which are usually "equilibrium" or "physiologically-resilient" species; (2) successional stages are characterized by organisms with differing population dynamics (*e.g.*, early stages are characterized by large populations of r-selected and opportunistic species; later stages include fewer opportunists, but have more K-selected and slow-growing species); and (3) episodes of succession take place when biotic interactions are more important, and alternate with periods when community dynamics are dominantly conformational and under the control of environmental parameters (*e.g.*, warm *vs.* cold seasons).

It is generally conceded that few convincing examples of ecologic succession have been documented from fossil deposits. Equivocal examples have been described by Walker and Alberstadt (1975), Walker and Parker (1976), and M. E. Johnson (1977). Significantly, Wilson (1985) reported recently what appears to be a plausible example of secondary ecologic succession involving cobble-encrusting organisms that inhabited an Upper Ordovician hardground, which suggests that examples may yet be found.

Community Response. Short-term changes in the composition and structure of communities resulting from allogenic environmental fluctuations, not leading to complete replacement of one community by another, are here termed *community response* (Table 1). Response probably alternates with ecologic succession in temperate estuarine and shallow marine settings, wherein seasonality is an important determinant of community structural changes (see Tenore, 1972; Boesch *et al.*, 1976). The resultant cyclic patterns produced by community response to gradually, sometimes seasonally, changing environmental rhythms or cues are here termed *pseudoseres.* Pseudoseres preserved as ecologically graded, microstratigraphic sequences of autochthonous fossils should be nearly impossible to differentiate from true successional sequences (seres), except where the effects of seasonality can be independently inferred from facies analysis and paleoclimatologic data. Sharp, aperiodic environmental change can have the impact of "downgrading" both successional and response sequences to earlier, less complex stages (*cf.* R. G. Johnson, 1972; Rollins *et al.*, 1979). Perhaps certain examples of short-term "allogenic succession" identified in the fossil record could be re-interpreted as preserved patterns of community response.

Patch Development. Little is known about the development, growth, and decline of benthic, soft-bottom patches (see Lorenz, 1973; Levin and Paine, 1974; Wilson, 1982). As defined here, patches are sites of prolonged occupation formed either by the amalgamation of seres resulting from ecologic succession, pseudoseres produced by community response cycles, or combinations of both (Table 1). Many thin shelly layers composed of autochthonous remains of ancient benthic communities probably represent patches of this type.

Community Replacement. Nearly all published descriptions of fossil succession are examples of community replacement (*e.g.*, Nicol, 1962; Donahue *et al.*, 1972; Goldring and Kaźmierczak, 1974; Bretsky and Bretsky, 1975; Walker and Alberstadt, 1975; Copper and Grawbarger, 1978; Toomey and Cys, 1979; Williams, 1980; Wolosz and Wallace, 1981). Many accounts of faunal transitions describe fossiliferous sequences compiled during long-term environmental changes affecting benthic community distributions in space and time, and thus represent additional examples of community replacement (Israelsky, 1949; Hudson, 1963; Kauffman, 1969; Stanton and Dodd, 1970; West, 1972; Alberstadt *et al.*, 1974; Donahue and Rollins, 1974; Shaver, 1974; Bromley, 1975; Lister, 1976; Bailey, 1977; Sundberg, 1980; Fürsich, 1981; Hickey and Younker, 1981; Isaacson and Curran, 1981; Beus, 1984). M. E. Johnson (1977) and Hoffman and Narkiewicz (1977) appear to have been the first workers to use the concept of replacement as it is applied in this paper. Rollins *et al.*, (1979) and Miller (1982) used the concept and terminology in a similar way for community transitions propelled by environmental changes.

The term "replacement" has been used as a label for other types of faunal transitions. One of the most common current uses of the term is in the form "ecologic replacement," which is sometimes used to mean faunal element substitution in evolutionary time occurring when extinctions vacate niches in communities (Boucot, 1975; Raup and Stanley, 1978). This is really a kind of community evolution, as is the "community replacement" of Sepkoski and Sheehan (1983).

I restrict the term community replacement to *long-term* (involving at least hundreds of generations of average benthos), *subevolutionary community transitions caused by either abrupt or gradual changes in environmental contexts.* The preserved patterns of community replacement, analagous to seres and pseudoseres, are here termed *community replacement sequences.* From a review of the literature on faunal transitions, it appears that replacement is a poorly understood, yet widespread and fundamental dynamic property of biotic communities. It may be the most important ecologic explanation for changes in autochthonous fossil associations sampled through vertical stratigraphic sequences unbroken by unconformities (Miller, 1986).

Community Evolution. Community evolution is at the opposite end of the time spectrum from succession and response. Temporal dynamics leading to evolutionary transitions in benthic communities, involving faunal element substitution, appearance of new types of communities, community structural divergences, and biogeographic displacements of communities, probably occur in time spans of 10^5 to 10^7 years. Resultant patterns could be termed *community lineages* (Table 1). Discussions of this type of community change can be found in Olson (1952), Shotwell (1964), Bretsky (1969), Valentine (1973), Boucot (1975), and Watkins and Boucot (1975).

IV. FLANNER BEACH FORMATION – CASE HISTORY STUDY OF COMMUNITY REPLACEMENT

General Stratigraphy. DuBar and Solliday (1963) proposed the name Flanner Beach Formation for fossiliferous muddy sand and silt-clay beds of Pleistocene age exposed along the lower Neuse River, in east-central North Carolina (Figure 1). The formation was subdivided into three informal members by Mixon and Pilkey (1976), including: (1) the Arapahoe sand, comprising barrier island deposits cropping out along both sides of the Neuse River near the Suffolk Scarp in Pamlico and Craven Counties; (2) the Newport sand, consisting of similar barrier sands underlying ridge-and-swale topography just south of the Newport River in Carteret County; and (3) the correlative, fossiliferous, muddy sand and silt-clay backbarrier deposits of the Beard Creek member. I proposed (Miller, 1985a) that these informal members be promoted to formal lithostratigraphic units, and also described and named a fourth member composed of pebbly, fossiliferous muddy sand (Smith Gut Member), located at the base of the formation, that reflects early transgressive open-bay conditions.

The Smith Gut, Beard Creek, and Arapahoe Sand members are well-exposed in the vicinity of Beard Creek in southern Pamlico County (Figure 2). In this area, the Smith Gut and Beard Creek members are very fossiliferous in places and contain both thick, laterally extensive shell beds (major complex and major simple shell accumulations of Kidwell, 1982), and thin lenses, pods, and single-shell stringers (minor complex and minor simple shell accumulations of Kidwell, 1982). All of the shell beds consist largely of the valves of the small mactrid clam, *Mulinia lateralis* (Say).

Beds within the Smith Gut and Beard Creek members were deposited in a spatial-temporal mosaic of bay and lagoonal environments about 200,000 years B.P., during a world-wide high stand of sea level. The Flanner Beach Formation rests disconformably on an older Pleistocene unit, the James City Formation, and is bordered on the east by younger Pleistocene deposits informally known as the "Core Creek sand" (DuBar and Solliday, 1963; Mixon and Pilkey, 1976). If reported amino acid and uranium-series dates for the Flanner Beach are accurate (McCartan *et al.*, 1982; Cronin *et al.*, 1984), the unit is time-correlative with van Donk's (1976) Atlantic Basin oxygen-isotope stage 7.

Methods. Deposited during a single transgressive-regressive cycle of Pleistocene coastal inundation, lasting perhaps tens-of-thousands of years, the Smith Gut and Beard Creek members were targeted for the study of long-period subevolutionary changes in deployment patterns of benthic communities. Rhythmic shelly layers in the Beard Creek area of Pamlico County were sampled at 20 to 40 cm vertical intervals (Figure 2). Fifteen, one-liter bulk samples of fresh sediment were washed on a sieve with 2 mm openings (measured diagonally). All identifiable fossil remains isolated in this way were identified, counted, and examined for signs of shell utilization by encrusting and boring organisms. Numbers of specimens were corrected to reflect the numbers of original individuals (*e.g.*, estimated number of bivalves of a particular species = number of articulated shells + [number of valves and valve fragments with beaks/2]), and these tallies were used to estimate relative abundances.

Taphonomy. Among the 75,748 identifiable specimens recovered from the samples, there are 143 species of animals, 111 of which are mollusks. Members of the Porifera, Cnidaria, Bryozoa, Annelida, Arthropoda, Echinodermata, and Chordata were also identified. An abundant and varied microbiota occurs in the Flanner Beach, but these organisms were not studied. Of all species identified, 41 appear to be exotic and derived from adjacent,

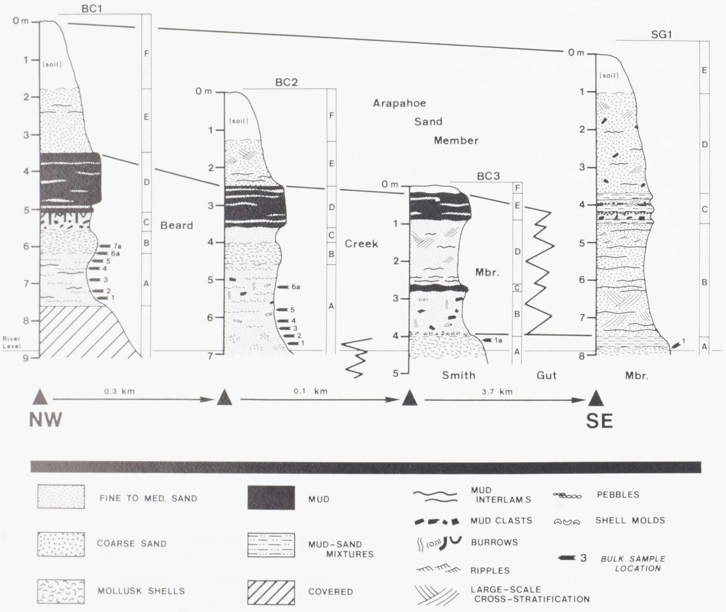

Figure 2. Stratigraphic panel diagram of bluff-line exposures of the Flanner Beach Formation in the vicinity of Beard Creek, southernmost Pamlico County, North Carolina. Exact locations of the measured sections are given in Appendix. Stratigraphic framework and depositional environments are discussed by Miller (1985a). Stratigraphic levels of bulk samples of fossils used in paleocologic analyses are indicated by arrows beside columns.

contemporary habitats, and 18 species were reworked from the subjacent James City Formation (Miller, 1984). All of the indigenous species are extant except one bivalve (Miller, 1985b). Complete inventories of fossils can be found in Miller (1984).

Explanations for the origin of shell beds in the Smith Gut and Beard Creek members must take into account the following characteristics: (1) all shelly accumulations, regardless of thickness, geometry, geographic extent, or stratigraphic elevation, are numerically dominated by *Mulinia lateralis*; (2) shell beds show evidence of varied scales of condensation and stratigraphic telescoping (see Kidwell, 1982); and (3) fossils are predominantly indigenous faunal elements, largely shiny and unabraded shells, in some places current-oriented and in others randomly oriented, and belong mainly to extant taxa that are known to inhabit mesohaline to polyhaline estuarine environments.

Mulinia lateralis is an opportunitic estuarine species capable of very rapid population growth owing to: (1) potential year-round gametogenesis (apparently controlled by ambient temperature); (2) very short generation times (about two months), typically with up to three generations/year; (3) rapid sexual maturation; and (4) a potential longevity of about two years (Calabrese, 1969; Levinton, 1970; Brande, 1979). Together with opportunistic soft-bodied metazoans, such as polychaete worms and amphipods, *M. lateralis* is among the first western Atlantic invertebrate species to reinvade modern benthic habitats that have been disturbed, destroyed, or ecologically "downgraded" (Rhoads, McCall, and Yingst, 1978).

In modern paralic environments along the American East Coast that are prone to aperiodic disturbances, such as those caused by increased sedimentation or the churning and resuspension of bottom sediments in storms, valves of *M. lateralis* are accumulating in large numbers (Biggs, 1967; Levinton, 1970). In samples from the Flanner Beach Formation, *M. lateralis* makes up 62 to 96% of individuals in fossil associations. Modern populations are especially sensitive to predation incurred as colonization of patches progresses, leading to large concentrations of dead shells (Virnstein, 1977). Most of the *M. lateralis* valves recovered from Flanner Beach samples, however, do not show *obvious* signs of predation (highest incidence is about 30%). Many of these incidences probably were not fatal and only involved nicks inflicted by crabs or fish along ventral edges of valves (see Bishop, 1975). It is unlikely that competition was a dominant factor shaping community structure in the shallow-water, estuarine benthic habitats of the Flanner Beach basin, in which the soft-bottom communities were highly, but not exclusively, physically controlled (see Sanders, 1968; R. G. Johnson, 1972). So it appears that allogenic, environmental processes might have caused the demise of localized *Mulinia* patches in this case.

Condensation and stratigraphic telescoping of fossiliferous beds can be caused by both biogenic and hydraulic/sedimentologic agencies, and by combinations of these kinds of processes (see Schäfer, 1972; Fürsich, 1978, 1982; Kidwell, 1982; Powell *et al.*, 1982; Kidwell and Jablonski, 1983, Table II). Thick shelly accumulations in the Smith Gut and Beard Creek members show signs of condensation resulting from low net sediment accumulation, but vary in terms of internal paleoecologic and biostratinomic complexity. These thick layers of shells have been intensively bioturbated, and microstratigraphic samples from them are likely to contain many generations of organisms and several seres/pseudoseres.

The primary concentrating process responsible for the thick shell beds in the Flanner Beach seems to have been low net sediment accumulation, as opposed to biogenic concentration, considering the environmental stratigraphic contexts: the thick shelly bed in the Smith Gut Member (Figure 2) was deposited during a rapid rise in sea level that quickly inundated a coastal lowland and subsequently created conditions of sediment starvation in a newly formed embayment, whereas the thick bed near the top of the Beard Creek Member (Figure 2) appears to be the result of sediment bypassing and/or winnowing in the environs of a tidal inlet in the nearby Arapahoe barrier (Miller, 1985a). In the course of accumulation, the beds were churned by the burrowing activities of infaunal organisms.

Deposition by transport and dumping or large-scale *in situ* winnowing during storms forming shelly lags does not seem likely because: (1) condition of most shells is unabraded (but almost all bivalves were disarticulated); (2) sediment size-grading and pronounced shell size-sorting were not observed, although these could result from bioturbation; (3) bottoms of beds do not show erosional or guttered surfaces; and (4) shell beds are never covered by plane-laminated or hummocky-laminated layers representing the waning phases of storms. The presence of a natural spectrum of growth stages among the more common species, and the low numbers of exotic and reworked shells compared to numbers of specimens belonging to indigenous estuarine taxa further argue against a storm origin for these thicker shell beds.

The thinner, tabular to lenticular shell beds and shelly pods within the Beard Creek Member (Figure 2) appear to be primarily the products of patch formation and other biogenic concentration processes, involving mixing of several superimposed seres/pseudoseres. Single-shell stringers seem to represent a single ecologic unit or event, but condensation and bioturbation have obliterated any internal ecologic grading that might originally have been present in the slightly thicker beds and lenses as a result of ecologic succession. Again, clear-cut evidence is lacking for storm influence in the formation of these thinner, more local accumulations of skeletons. It is likely that the backbarrier setting was somewhat protected from the effects of storm surges, but, alternatively, evidence of storm reworking and deposition may have been erased by biogenic alteration of sedimentary structures.

Surrounding the thinner shell beds in the Beard Creek Member are sparsely fossiliferous muddy sands containing only a few scattered shells. These intervals are either the least condensed and time-averaged fossil deposits in the Flanner Beach Formation, or represent intervals (areas of substrate) between periods (loci) of patch development. Both local stratigraphic expansion and temporary reduction of biotic input of skeletons may have been involved. The "barren" intervals might also represent bioturbated blankets of storm-deposited sediments.

In summary, the following factors most strongly influenced the origin and preservation of shelly concentrations in bay and backbarrier lagoonal facies of the Flanner Beach Formation: (1) telescoping/expansion of local stratigraphic sequences as a result of variable net sediment accumulation; (2) local increases in the production of skeletons owing to outbreaks of skeletalized, opportunistic clams and the subsequent recruitment of other shelled taxa during the development of patches; and (3) biogenic mixing of microstratigraphic levels and concentration of shells. Sedimentary condensation was the dominant factor in the formation of thick, major complex and major simple shell beds; whereas biogenic processes of concentration probably predominated in the formation of thin, minor complex and minor simple shell beds. Storm-related disturbance also could have been important, but strong evidence of this is lacking.

Paleosynecology. Preserved patterns of original community composition and structure are best represented among taxonomic groups that possess durable, mineralized skeletons, which translate into fossil remains with minimal information loss (Lawrence, 1968; Valentine, 1972; Schopf, 1978). Therefore, analysis of fossil associations focused mainly on gastropod and bivalve mollusks. Recognition of paleocommunity properties and patterns of change with time should have a relatively high degree of reliability in bay and lagoonal depositional sequences because: (1) fossils are derived from organisms that lived, died, and were buried essentially in place (Johnson, 1965; Warme, 1969; Warme *et al.*, 1976); (2) an appreciable fraction of original community components are mollusks, which have varied modes of feeding and substrate-niche preferences, and are easily fossilized; (3) short-term population variations, diversity oscillations, and seasonal effects are averaged into composite synecologic pictures of original community composition and structure during the gradual, *in situ* accumulation of shells (Walker and Bambach, 1971; Warme *et al.*, 1976; Peterson, 1977); and (4) net sediment accumulation rates in backbarrier environments in general could potentially preserve patterns of community temporal dynamics such as replacement, and rarely succession and response, and the resultant sequences normally contain few extremely condensed intervals or major stratigraphic gaps (*cf.* shelly open-shelf sequences: Schindel, 1980).

The paleosynecologic analysis of Flanner Beach fossils uses compositional attributes of fossil associations (taxonomic composition, abundance, species richness, and dominance and diversity of mollusks), trophic and substrate-niche proportions, and general patterns of predation and overgrowths of skeletons. When preserved community patterns are traced through stratigraphic frameworks, it is possible to document the synecologic histories of depositional sequences (Miller, 1982), and inferences concerning the causes of community change through time can be tested.

Compositional attributes were assessed by the following standard methods: (1) compilation of species lists of indigenous faunal components; (2) estimation of absolute and relative abundance of individuals based on counts of skeletal remains, corrected to relate numbers of skeletal parts to original numbers of individuals in the living community; (3) ranking taxa using absolute abundances; (4) determination of overall species richness (total number of indigenous species) and molluscan species richness; and (5) calculation of molluscan dominance, diversity, and evenness indices. Molluscan dominance for each sample was computed by substitution in the equation:

$$C_m = \sum_{i=1}^{S_m} p_i ,$$

where S_m is species richness of mollusks and p is the proportion of individuals belonging to the ith molluscan species. Molluscan diversity was computed by substitution in the Shannon-Weaver equation:

$$H' = -\sum_{i=1}^{S_m} p_i \ln p_i ,$$

where ln is the natural logarithm. Molluscan evenness was calculated by substitution in the equation:

$$E_m = H_m / \ln S_m .$$

Use of all three equations for paleocommunity analysis is described in Dodd and Stanton (1981). Only mollusks are used in the computation of these indices in this study because original species richness and abundance in dead shell accumulations of mollusks derived from living communities should be reliably represented in fossil associations deposited in protected bay and lagoonal settings. Estimates of richness and abundance for other important groups of organisms (*e.g.*, cirripeds, bryozoans) can be only approximate owing to dismemberment of skeletons or fragmentation of colonies after death. Table 2 gives indices calculated for all samples. Table 3 lists the most abundant species and average compositional indices for fossil associations recognized in bulk samples from the Smith Gut and Beard Creek members.

Trophic proportions were estimated for each sample using all indigenous faunal components by employing the methods of paired substrate-niche and feeding behavior ternary diagrams, as described by Scott (1976, 1978). Because nearly all indigenous fossil components belong to extant species, generalized substrate and feeding categories could be determined using the literature on modern estuarine and marine organisms from the western Atlantic Ocean and Gulf of Mexico. Figure 3 shows the "descriptive trophic structure" (Scott, 1978) of fossil associations including the most abundant mollusk, *Mulinia lateralis*; Figure 4 shows trophic structure with *M. lateralis* excluded.

A series of comparative studies of living benthic communities and their associated

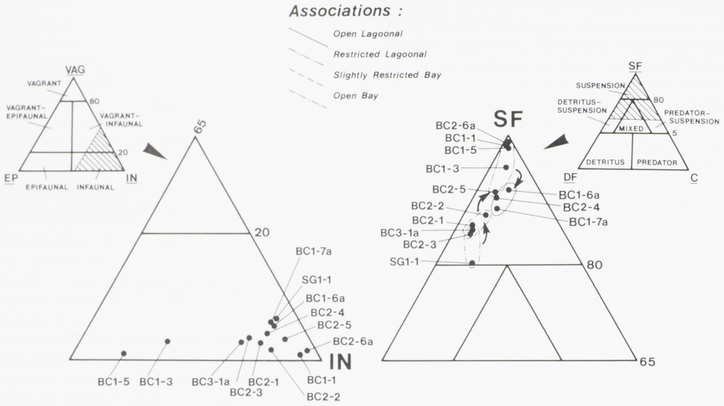

Figure 3. Descriptive trophic structure of Flanner Beach fossil associations. Sample numbers correspond to those used in Figure 2. Method of constructing paired ternary diagrams to represent preserved trophic proportions is described in Scott (1976, 1978). Symbols have the following meanings: *VAG*, vagrant; *EP*, epifaunal; *IN*, infaunal; *SF*, suspension-feeding; *DF*, detritus feeding and algal grazing; *C*, carnivorous and parasitic. Detailed views of the infaunal corner of substrate-niche and suspension-feeding corner of feeding behavior diagrams are shown.

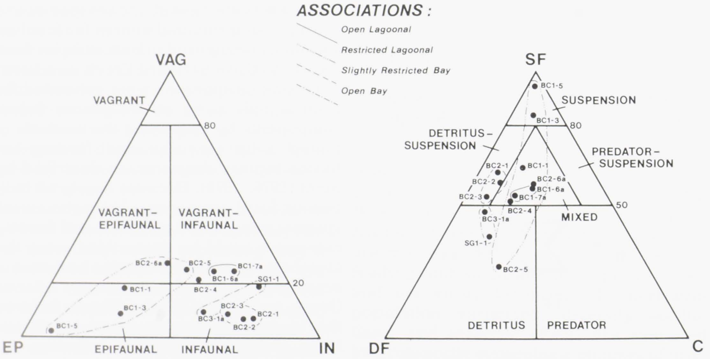

Figure 4. Descriptive trophic structure with *Mulinia lateralis* deleted. Sample numbers refer to Figure 2, and method of constructing diagrams and symbols used are same as in Figure 3.

TABLE 2. Quantitative compositional attributes of fossil associations from the Flanner Beach Formation. Symbols are defined at foot of table. Samples are listed in stratigraphic order (see Figure 2).

Sample	Fossil Association	S'	S	S_{ex}	S_{re}	S_m	C_m	H'_m	E_m
BC1-7a	Open lagoonal	60	59	2	0	49	0.85	1.07	0.27
BC1-6a	Open lagoonal	55	48	7	0	38	0.69	0.87	0.24
BC1-5	Restricted lagoonal	27	22	5	0	19	0.90	0.31	0.11
BC1-4*	Restricted lagoonal	7	6	1	0	5	0.73	0.61	0.38
BC1-3	Open lagoonal	51	43	7	0	35	0.72	0.78	0.22
BC2-6a	Restricted lagoonal	31	22	9	0	19	0.95	0.17	0.06
BC1-2*	Restricted lagoonal	18	16	2	0	15	0.37	1.56	0.58
BC1-1	Restricted lagoonal	20	17	2	0	16	0.96	0.13	0.05
BC2-5	Restricted lagoonal	23	19	3	0	18	0.81	0.57	0.20
BC2-4	Transitional (between slightly restricted bay and restricted lagoonal)	31	28	3	0	25	0.74	0.80	0.25
BC2-3	Slightly restricted bay	43	39	1	2	32	0.56	1.23	0.35
BC2-2	Slightly restricted bay	68	56	8	7	41	0.58	1.15	0.31
BC3-1a	Open bay	87	56	18	15	42	0.63	1.04	0.28
BC2-1	Slightly restricted bay	56	49	2	6	35	0.47	1.31	0.37
SG1-1	Open bay	107	54	38	20	44	0.49	1.49	0.39

Symbols used in column headings:

S' – uncorrected, raw species richness of fossil deposit; because in a few instances species could not be related to original habitats or stratigraphic levels, S' is not always exactly equal to $S + S_{ex} + S_{re}$ (see below)
S – corrected species richness of the indigenous fossil association; environmentally exotic and reworked species eliminated
S_{ex} – richness of contemporary, environmentally exotic species
S_{re} – richness of reworked species from the subjacent James City Formation
S_m – richness of indigenous molluscan species; used in calculations of C_m, H'_m, and E_m (see text)
C_m – molluscan species dominance
H'_m – molluscan species diversity
E_m – molluscan species eveness
* – sample from an expanded interval between shelly accumulations; not time-averaged to the same degree as other shelly layers

dead shell accumulations in modern environments has shown that preserved trophic proportions are usually poor representations of original trophic structure, and that reconstruction of original trophic dynamics of holistic communities based on these patterns is generally not possible (Stanton, 1976; Stanton and Dodd, 1976). Trophic structure studies still hold promise in paleoenvironmental analyses that utilize fossil associations from protected depositional settings, and in documentation of the complexity of species interactions in sequences of ancient communities (see Scott, 1978; Stanton and Nelson, 1980). Descriptive trophic structure thus has value in yielding additional paleosynecologic descriptors useful in tracing fossil associations through bay and lagoonal deposits in the Smith Gut and Beard Creek members.

Predation and overgrowth analysis of four samples, representing each of the fossil associations, was undertaken to document changes in patterns and complexity of biotic interactions and dead-shell utilization through time. Results are presented in Table 4. Like descriptive trophic structure, changes in the patterns of predation and skeletal overgrowths between fossil associations in vertical stratigraphic sequences are used to trace changes in paleocommunities through time.

TABLE 3. Most common taxonomic components of fossil associations in the Smith Gut and Beard Creek members. Only taxa comprising ≧0.5% of individuals within at least one sample are listed, and all symbols are defined at bottom of table. Complete faunal inventories for each sample, including rare species, are listed in Miller (1984, Appendix III).

Species	Type of Organism	Rank*	Average Absolute Abundance	Average Relative Abundance	Substrate-Niche/Feeding Category
I. *OPEN BAY ASSOCIATION* (2 SAMPLES)					
Mulinia lateralis	Bi	1	1685.5	72.4%	IN/SF
Nuculana acuta	Bi	2	161.5	6.9	IN/DF
Balanus spp.	Ci	3	110.0	4.7	EP/SF
Tellina texana	Bi	4	82.5	3.5	IN/DF
Acteocina canaliculata	Ga	5	50.0	2.1	VAG/C
Ensis directus	Bi	6	34.5	1.5	IN/SF
Corbula contracta	Bi	7	30.0	1.3	IN/SF
Solen viridis	Bi	8	22.0	0.9	IN/SF
Nucula proxima	Bi	8	22.0	0.9	IN/DF
Yoldia limatula	Bi	9	19.5	0.8	IN/DF
Pandora trilineata	Bi	10	15.5	0.7	IN/SF
Mysella planulata	Bi	11	14.0	0.6	EP/SF
Abra aequalis	Bi	12	13.5	0.6	IN/DF
Holoporella spp. (3?)	Br	13	12.0	0.5	EP/SF
Anadara transversa	Bi	14	10.5	0.5	IN/SF
Nassarius trivittatus	Ga	15	9.5	0.4	VAG/DF
Electra spp. (2?)	Br	16	8.5	0.4	EP/SF
Macoma tenta	Bi	17	7.0	0.3	IN/DF
Diplodonta notata	Bi	17	7.0	0.3	IN/SF
Erycina floridana	Bi	18	6.5	0.3	IN?/SF?
Crepidula sp.	Ga	19	6.0	0.3	EP/SF
$\bar{S} = 55$	$\bar{S}_m = 43$		$\bar{C}_m = 0.56$	$\bar{H}'_m = 1.26$	
II. *SLIGHTLY RESTRICTED BAY ASSOCIATION* (3 SAMPLES)					
Mulinia lateralis	Bi	1	1582.7	70.4%	IN/SF
Ensis directus	Bi	2	226.0	10.1	IN/SF
Balanus sp.	Ci	3	96.0	4.3	EP/SF
Tellina texana	Bi	4	79.3	3.5	IN/DF
Nuculana acuta	Bi	5	58.0	2.6	IN/DF
Nucula proxima	Bi	6	41.7	1.9	IN/DF
Abra aequalis	Bi	7	32.0	1.4	IN/DF
Yoldia limatula	Bi	8	21.3	0.9	IN/DF
Solen viridis	Bi	9	20.3	0.9	IN/SF
Acteocina canaliculata	Ga	10	17.3	0.8	VAG/C
Corbula contracta	Bi	11	14.0	0.6	IN/SF
Busycon sp.	Ga	12	13.7	0.6	VAG/C
Membranipora spp. (2?)	Br	13	10.7	0.5	EP/SF
Holoporella spp. (2?)	Br	13	10.7	0.5	EP/SF
Mysella planulata	Bi	14	9.7	0.4	EP/SF
Anadara transversa	Bi	15	6.0	0.3	IN/SF
Mitrella lunata	Bi	16	5.3	0.2	VAG/C?
Busycon sp. cf. *B. carica*	Ga	17	4.0	0.2	VAG/C
$\bar{S} = 48$	$\bar{S}_m = 36$		$\bar{C}_m = 0.54$	$\bar{H}'_m = 1.23$	

(Continued next page)

III. *TRANSITIONAL ASSOCIATION* (1 SAMPLE)

Mulinia lateralis	Bi	1	861	80.7	IN/SF
Balanus sp.	Ci	2	54	5.1	EP/SF
Tellina texana	Bi	3	39	3.7	IN/DF
Ensis directus	Bi	4	18	1.7	IN/SF
Acteocina canaliculata	Ga	4	18	1.7	VAG/C
Nuculana acuta	Bi	5	10	0.9	IN/DF
Corbula contracta	Bi	5	10	0.9	IN/SF
Solen viridis	Bi	6	9	0.8	IN/SF
Nucula proxima	Bi	7	7	0.7	IN/DF
Mysella planulata	Bi	7	7	0.7	EP/SF
Terebra dislocata	Ga	8	6	0.6	VAG/C
Abra aequalis	Bi	9	5	0.5	IN/DF

$S = 28$ $S_m = 25$ $C_m = 0.74$ $H'_m = 0.80$

IV. *RESTRICTED LAGOONAL ASSOCIATION* (4 SAMPLES)

Mulinia lateralis	Bi	1	1592.3	89.4%	IN/SF
Balanus sp.	Ci	2	145.0	8.1	EP/SF
Acteocina canaliculata	Ga	3	10.3	0.6	VAG/C
Tellina texana	Bi	4	9.0	0.5	IN/DF
Ensis directus	Bi	5	8.5	0.5	IN/SF
Nassarius trivittatus	Ga	6	6.8	0.4	VAG/DF
Nucula proxima	Bi	7	3.5	0.2	IN/DF
Nuculana acuta	Bi	8	3.3	0.2	IN/DF
Abra aequalis	Bi	9	2.3	0.1	IN/DF

$\bar{S} = 20$ $\bar{S}_m = 18$ $\bar{C}_m = 0.91$ $\bar{H}'_m = 0.30$

V. *OPEN LAGOONAL ASSOCIATION* (3 SAMPLES)

Mulinia lateralis	Bi	1	4436.3	78.0%	IN/SF
Balanus sp.	Ci	2	321.3	5.7	EP/SF
Ensis directus	Bi	3	320.0	5.6	IN/SF
Tellina texana	Bi	4	162.0	2.8	IN/DF
Acteocina canaliculata	Ga	5	124.0	2.2	VAG/C
Corbula contracta	Bi	6	58.7	1.0	IN/SF
Nassarius trivittatus	Ga	7	54.0	0.9	VAG/DF
Mysella planulata	Bi	8	44.7	0.8	EP/SF
Solen viridis	Bi	9	36.3	0.6	IN/SF
Nucula proxima	Bi	10	29.3	0.5	IN/DF
Nuculana acuta	Bi	11	29.0	0.5	IN/DF
Membranipora sp.	Br	12	25.0	0.4	EP/SF
Terebra dislocata	Ga	13	24.0	0.4	VAG/C
Abra aequalis	Bi	14	21.3	0.4	IN/DF

$\bar{S} = 50$ $\bar{S}_m = 40.7$ $\bar{C}_m = 0.75$ $\bar{H}'_m = 0.91$

EXPLANATION OF SYMBOLS:

* – Based on average absolute abundance

Types of organisms:
Bi – bivalve mollusk
Ga – gastropod
Ci – cirriped crustacean
Br – bryozoan

Generalized substrate-niche designations:
IN – infaunal, for the most part sedentary or ranging over short distances
EP – epifaunal, for the most part sedentary or attached
VAG– vagrant, capable of frequent or prolonged movements

(Continued next page)

Generalized feeding behavior designations:
SF – suspension feeder
DF – detritus feeder, including herbivores and microphagous scavengers
C – carnivorous, including parasites and macrophagous scavengers

Compositional indices (see text):
$\bar{S}$ – average overall species richness
$\bar{S}_m$ – average richness of molluscan species
$\bar{C}_m$ – average dominance of molluscan species
$\bar{H}'_m$ – average species diversity of mollusks

Fossil Associations. As used here, a fossil association is the *preserved remains of a single, once-living biotic community.* Five associations were recognized in bulk samples. These included, in ascending stratigraphic order: (1) open bay association; (2) slightly restricted bay association; (3) a transitional association (between slightly restricted bay and restricted lagoonal); (4) restricted lagoonal association; and (5) open lagoonal association. These associations were identified based on taxonomic composition, species-abundance distributions, preserved trophic structure, preserved patterns of species interactions, and relationships to original substrates. The five slightly different associations so recognized appear to be derived from a continuum of at least three estuarine benthic communities arrayed along environmental gradients in average salinity, degree of overall environmental rigor (disturbance, seasonality), and substrate properties. End-members in this model continuum were: (1) a muddy-sand-bottom, polyhaline, open bay community; (2) a sand-bottom, mesohaline, restricted lagoonal community; and (3) a shelly-bottom, polyhaline, open lagoonal community. Flanner Beach fossil associations are discussed briefly below.

Overall species richness, molluscan species richness, and molluscan diversity were highest in open bay associations from the Smith Gut Member (Table 3, Figure 5). As in all associations from the Flanner Beach, *Mulinia lateralis*, a shallow-infaunal suspension-feeder, was by far the numerically dominant component. Unlike other associations, however, the infaunal detritus-feeder *Nuculana acuta* ranked second, with balanid barnacles (possibly commensal with *M. lateralis*; see Brande, 1982), *Tellina texana* (another detritus-feeding, infaunal clam), and *Acteocina canaliculata* (a diminutive, probably carnivorous, opisthobranch snail) ranking third through fifth, respectively. Minor components included a variety of predatory snails, many kinds of clams, and a rare ahermatypic coral (*Astrangia* sp.). Species richness among bryozoans was relatively high with up to eight species. Using the descriptive trophic classification of Scott (1976), open bay associations can be classified as infaunal-suspension feeding; if *M. lateralis* is deleted, an infaunal-detritus feeding classification results (Figures 3, 4). Predation traces and epizoan overgrowths were varied and numerous (Table 4), suggesting patterns of species interaction and dead-shell utilization that were the most complex of any fossil associations from the Flanner Beach. Of all the associations sampled, open bay associations reflect conditions of average salinity and environmental stability closest to those of open shelf settings.

Stratigraphic levels just above the Smith Gut Member contained slightly restricted bay associations (Table 3; Figure 5), characterized by slightly lower overall species richness, molluscan species richness, and molluscan diversity. *Mulinia lateralis* was again the numerically dominant organism, but *N. acuta* receded to fifth in rank. The clam *Ensis directus*, a deep-burrowing suspension feeder as an adult, was second in abundance, followed by another suspension feeder, *Balanus* sp.; *Tellina texana* ranked fourth and *A. canaliculata* dropped to tenth. When *M. lateralis* is included in the trophic classification, associations are infaunal-suspension feeding; without the opportunistic mactrid, an infaunal detritus-suspension feeding trophic structure is indicated (Figures 3, 4). Variety and abundance of predation marks and epizoan overgrowths are diminished compared to open bay associations (Table 4)

TABLE 4. Patterns of predation, skeletal overgrowth, and dead-shell utilization in fossil associations from the Smith Gut and Beard Creek members. Patterns in the highest ranked host species are given for representative samples of each type of association. Sources used to identify predation traces and epizoans/endozoans included: Canu and Bassler, 1923; Boekschoten, 1966, 1967; Miller and Brown, 1979; Boucot, 1981. Symbols are defined at bottom of table.

TYPE OF PREDATION SIGN OR EPILITHIC/ENDOLITHIC ORGANISM HOST (with rank)	biogenic shell breakage, unrepaired (decapod crustaceans)	biogenic shell breakage, repaired	snail drillholes (naticid mesogastropods)	*Electra* pits (cheilostome bryozoan)	"*Spathipora*" borings (ctenostome bryozoan)	*Polydora* borings (polychaete annelid)	*Cliona* borings (demosponge)	*Holoporella* encrustations (cheilostome bryozoan)	*Smittina* encrustations** (cheilostome bryozoan)	balanid bases (cirriped crustacean)	balanid attachment scars
I. OPEN BAY ASSOCIATION (SAMPLE SG1-1, FIGURE 2)											
Mulinia lateralis (1)	A*	R	C	R^i	R	R	R	R	R^i	–	R
Nuculana acuta (2)	C	R	R	–	–	–	R*	–	–	–	–
Tellina texana (3)	C*	R	R	R	R	–	R*	–	–	–	–
Acteocina canaliculata (4)	C	C	C	–	R	–	–	–	–	–	–
Ensis directus (5)	A*	–	–	–	–	–	–	–	–	–	–
II. SLIGHTLY RESTRICTED BAY ASSOCIATION (SAMPLE BC2-2, FIGURE 2)											
Mulinia lateralis (1)	A	R	R	R^i	R	R	–	–	–	R	C
Ensis directus (2)	A*	R	–	R^i	–	–	–	–	–	–	–
Tellina texana (3)	A*	R	R	–	–	–	–	–	–	–	–
Balanus sp. (4)	C*	–	R	R	–	–	–	–	–	–	–
Nucula proxima (5)	C*	R	R	–	–	–	–	–	–	–	–
III. RESTRICTED LAGOONAL ASSOCIATION (SAMPLE BC1-1, FIGURE 2)											
Mulinia lateralis (1)	A	R	C	–	–	–	–	–	–	R	R
Balanus sp. (2)	–	–	–	–	–	–	–	–	–	–	–
Tellina texana (3)	C*	–	R	–	–	–	–	–	–	–	–
Acteocina canaliculata (4)	R	R*	–	–	–	–	–	–	–	–	–
Nuculana acuta (4)	R	–	R	–	–	–	–	–	–	–	–
Nassarius trivittatus (4)	A	C	C*	–	–	–	–	–	–	–	–
Ensis directus (5)	C*	–	–	–	–	–	–	–	–	–	–
IV. OPEN LAGOONAL ASSOCIATION (SAMPLE BC1-7a, FIGURE 2)											
Mulinia lateralis (1)	A	C	R	R^i	–	R	–	–	–	–	C
Ensis directus (2)	A*	R	–	R^i	–	–	–	–	–	–	–
Tellina texana (3)	A*	R	C	R	–	–	–	–	–	–	–
Balanus spp. (4)	C*	–	R	–	–	–	–	–	–	–	–
Acteocina canaliculata (5)	C	C	R	–	–	–	–	–	–	–	–

Explanation of Symbols:

A – abundant, > 25% of host shells show predation marks or epilithic/endolithic infestations

C – common, 5 to 25% of host shells

R – rare, < 5% of host shells

* – some examples may be due to non-biogenic damage to shell caused by post-entombment compressional breakage or chemical dissolution of shells

** – possibly an environmentally exotic or reworked faunal element

i – interior as well as exterior surfaces of host shells bored/infested

– – not observed

and bryozoan species richness declines. Slightly reduced or more frequently fluctuating ambient salinities appear to have controlled benthic community structure during accumulation of the slightly restricted bay association. This is supported by limited oxygen-isotope profiling of the Beard Creek Member using *M. lateralis* valves (Figure 6).

One sample contained a transitional fossil association that shared attributes of both the slightly restricted bay and restricted lagoonal associations (Table 3). Compositional indices had values intermediate between those of associations preserved at slightly higher and lower stratigraphic levels within the Beard Creek Member. As always, *M. lateralis* was by far the dominant component, with *Balanus* sp., *T. texana*, *E. directus*, and *A. canaliculata* following in rank order. Bryozoans were not found. With *M. lateralis* included, the transitional association can be classified as infaunal-suspension feeding; with the dominant clam excluded, the association is vagrant-infaunal mixed feeding (Figures 3, 4). This association of fossils reflects a gradual transition in all preserved structural attributes from conditions of higher salinity, probably polyhaline environments, to lower salinity, mesohaline environments. Its properties are significant because they reflect community reorganization "in progress" within a gradually changing backbarrier setting.

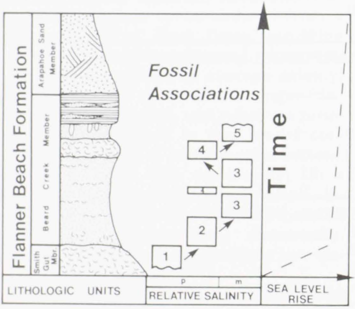

Figure 5. Community replacement sequence in the Flanner Beach Formation. Stratigraphic column is idealized, and sea level curve is shown as a dashed line. Symbols have the following meanings: (1) open bay fossil association; (2) slightly restricted bay association; (3) restricted lagoonal association; (4) open lagoonal association; (5) lagoonal firm-ground association; (p) polyhaline; (m) mesohaline. (Stratigraphic column not to scale.)

Lowest values of overall species richness, molluscan species richness, and molluscan diversity are found in the restricted lagoonal association. Molluscan dominance reaches its highest levels (Table 3; Figure 5) because samples contain the valves of *M. lateralis* and very little else. *Balanus* sp. ranked second, and *A. canaliculata*, *T. texana*, and *E. directus* were third through fifth. *Nuculana acuta* fell to eighth in rank. The only bryozoan recovered from samples was *Membranipora* sp. With *M. lateralis* included, descriptive trophic structure is again infaunal-suspension feeding; without *M. lateralis* the classification of Scott (1976) cannot be easily applied because points do not cluster in any of the field divisions on ternary diagrams (Figures 3, 4). The simplest patterns of predation and skeletal overgrowths were observed in this association, although *number* of obvious predation traces appeared to be as high as in the open bay association (Table 4). Preserved structural attributes indicate accommodation to the most rigorous environment of all fossil associations studied from the Flanner Beach Formation, and probabaly to the lowest levels of average salinity (as indicated in oxygen-isotope profile, Figure 6). Also, entombing sediments become much less muddy compared to lower stratigraphic levels.

Near the top of the Beard Creek Member is a thick shell bed containing an open lagoonal association, indicative of a return to higher levels of average salinity and greater community complexity. One thin shell bed near the middle of the Beard Creek Member also contained this association (see Figure 5). Overall species richness and molluscan species richness return to levels comparable to values from the open bay association. Molluscan dominance and diversity are similar to values for the transitional association (Table 3). Samples contained three bryozoan species, on average. Although examples of predation traces and epizoan encrustations are numerous, earlier levels of complexity of species interactions and dead-shell utilization are not re-attained (Table 4). Abundance of *M. lateralis* causes the high molluscan dominance values. As in the transitional restricted lagoonal associations, balanid barnacles rank second, and *E. directus*, *T. texana*, and *A. canaliculta* follow in rank abundance. Numerically minor components include several species of carnivorous snails, many clams, and a rare coral (*Astrangia* sp.). With *M. lateralis* included, this association can be described as infaunal-suspension feeding; if the dominant clam is deleted, it is epifaunal to vagrant-infaunal, mixed to suspension-feeding (Figures 3, 4). The open lagoonal assocation reflects periodic re-establishment of more open circulation and higher, probably polyhaline salinities (supported by results of $^{18}O/^{16}O$ profiling, Figure 6), resulting from opening and migration of tidal inlets in the nearby Arapahoe barrier to the east. Substrates in this area were shelly sands, considering the abundance of fossil shells in samples.

Other fossil associations in the Flanner Beach Formation include a poorly preserved, lagoonal firm-ground association with *Cyrtopleura* sp., stratigraphically above the open lagoonal association (Figure 5). Beds containing this association are deeply weathered and were not used in the paleoecologic analysis. Notes on other fossil associations in the Flanner Beach are given in Miller (1984).

Gradual Community Replacement Sequence. Probably as a response to changes in circulation patterns and salinity levels controlled by the development and modification of nearby barrier islands, but also as a result of related local changes in substrate characteristics, paleocommunities of the Flanner Beach Formation changed through time. This is shown by the gradual transition of fossil associations preserved in the Smith Gut and Beard Creek members (Figure 5). The sequence of associations: (1) incorporates the greater part of an interglacial transgressive depositional sequence, which represents an estimated 2 x 10^4 years of environmental history (Miller, 1984); (2) does not include faunal shifts that correspond to sharp changes in sediment textures and assemblages of sedimentary structures; and (3) does not result from stratigraphic gaps in the section. Stratigraphic, isotopic, and paleontologic evidence point to gradual alteration in the environment of deposition (and organism habitats) through time as the cause of faunal transitions within the bay and backbarrier facies. As such, the sequence of associations is an example of gradual community replacement, and not ecologic succession or other succession-like phenomena.

The open bay association, from the lowest stratigraphic levels in the bluffs along the north side of the Neuse River, is the most species-rich and diverse of all the fossil associations studied. It was derived from a diverse, relatively complex, estuarine seafloor community that inhabited muddy, shelly sand substrates in waters of

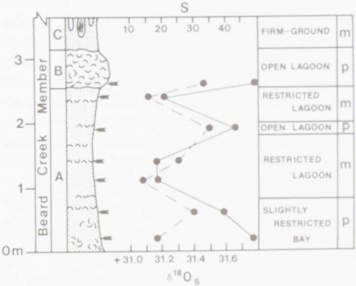

Figure 6. Diagram showing oxygen-isotope deviations ($\delta^{18}O_s$), relative to the SMOW standard (dashed line), and overall species richness (*S*) of fossil associations (solid line) plotted against stratigraphic elevation in a composite of columns BC1 and BC2 (Figure 2), beginning at base of the Beard Creek Member. Note that high values in $\delta^{18}O_s$ using *Mulinia lateralis* valves are usually matched by species-richness increases. Considering environment of deposition and paleoecologic properties, this pattern is probably indicative of cyclic changes in average salinity levels. Column at right lists fossil associations identified in bulk samples; *p*, polyhaline environment, *m*, mesohaline environment.

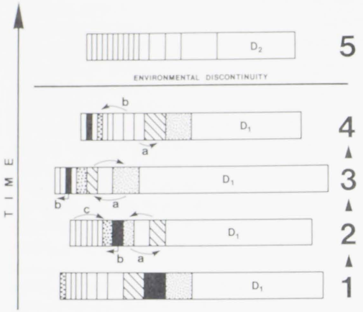

Figure 7. Conceptual model of gradual community replacement. Each numbered bar represents a community and the bar segments represent species abundances. As environmental qualities gradually change, one community gradually replaces another in a particular area. Stages in the sequence include: (1) initial appearance of a high-dominance community in a newly opened environment, with D_1 standing for a numerically dominant species and patterned bar segments indicating other less numerous faunal components; (2) the first community is then replaced by a similar community with slightly different structural properties, in which subdominant taxa have exchanged rank-abundance positions (a), certain taxa begin long-term demotion tends in abundance (b), and some lower rank taxa undergo jumps in abundance (c); (3) the second community is next reorganized to form a third community in which subdominant taxa re-exchange rank positions (a), demotion trends for some species continue (b), and some species completely disappear locally; (4) then another slightly different community appears with single-level shifts in rank abundance (a), abundance demotions (b), and changes in numerical importance of the dominant organism. Finally, community (5) replaces community (4) during a sharp change in environmental contexts, leading to species turnover of nearly all taxonomic components of the antecedent community, including the replacement of dominant organism, D_1, by the new dominant organism, D_2.

near-normal marine salinity. As the Arapahoe-Newport barrier complex began to develop just to the east of the study area, geomorphic configuration of the coastline changed from that of an open embayment to a slightly restricted sound. Concomitant with a change in circulation patterns in this progressively more isolated estuarine basin was a gradual lowering of average salinity levels. At this point the open bay association was succeeded by a slightly restricted bay association in the vicinity of Beard Creek. This association is not as rich in species and not as diverse as the antecedent association, and reflects a community with slightly modified compositional and structural attributes.

As lagoonal sediments accumulated in what had gradually become a well-isolated backbarrier basin, the remains of a second, even less species-rich and diverse community were deposited. The restricted lagoonal association indicates an environment in which salinity levels reached their lowest on average, but probably fluctuated widely as a result of seasonal runoff from the mainland. Substrates had become less muddy, as shown by matrix surrounding fossils.

That circulation patterns again changed and occasional increases in average salinity occurred, probably linked to the opening, migration, and closing of tidal inlets in the Arapahoe-Newport barrier, are indicated by a moderately species-rich and diverse open lagoonal association near the top of the Beard Creek Member (Figure 5). This association exhibits preserved compositional and structural attributes similar, but not identical, to those of open and slightly restricted bay associations found at lower stratigraphic levels in the Flanner Beach. Detritus feeders were much less important in the open lagoonal association, however, because of changes from muddy sand to shelly sand substrates, and because of an increase in hydraulic energy related to shoaling and proximity to active inlets. Species-richness and diversity values are comparable to those of the open and slightly restricted bay associations because all three fossil associations were derived from communities that inhabited polyhaline waters. They differ enough in taxonomic composition, preserved trophic structure, and substrate types to be regarded as having been derived from slightly different, original communities.

V. MECHANISMS OF COMMUNITY REPLACEMENT

Long-Period, Subevolutionary, Community Temporal Dynamics. There seem to be two principal ways that replacement of communities could take place, depending upon rapidity and severity of habitat alteration. Sharp changes in local environments should eliminate most resident organism populations, and, when new environmental parameters are established, attritional replacement of communities through *species turnover* should occur. Very slow, continuous environmental alterations should lead to less catastrophic replacement sequences typified by *reorganization of species-abundance distributions* (see May, 1975) within established communities. Both turnover and reorganization probably operate together with one or the other mechanism being dominant in most types of changing environments.

R. G. Johnson (1972, p. 156-158) proposed a model of benthic community transition in shifting environments, adopted and elaborated by Rollins *et al.*, (1979), which described conceptually the mechanism of subevolutionary species turnover involving two adjacent, soft-bottom communities. Although Johnson regarded this type of change as a kind of environmentally-driven succession, it is a species-by-species turnover process (see Rollins *et al.*, 1979, p. 89-90). Hoffman and Narkiewicz (1977) discussed turnover in terms of developmental stages involving replacement of Paleozoic reefs. M. E. Johnson (1977) described water depth-controlled replacement of brachipods in Silurian benthic communities. A model proposed by Rollins and Donahue (1975) relates changing communities to transgressive-regressive depositional cycles, and is esentially a generalized conceptual model of replacement related to cycles of changing relative sea level. Rollins *et al.*, (1979) described changes in the composition and structure of their *Chonetinella-Septopora* Community, from the Upper Pennsylvanian Cambridge Limestone, as an example of succession. But this could be viewed alternatively as an example of gradual community replacement by reorganization considering the time-span and kinds of changes in faunal composition that were involved.

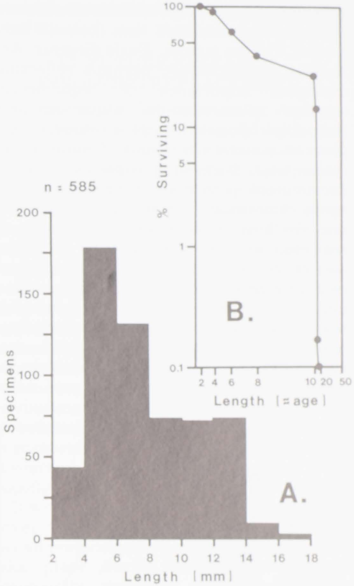

Figure 8. Normal population structure of *Mulinia lateralis* from a slightly restricted bay association (sample BC2-3, Figure 2). (A), size-frequency distribution of right valves; (B), survivorship curve based on (A) (both diagrams constructed using methods described by Dodd and Stanton, 1981). Compare with Figure 9.

The community replacement sequence in the Flanner Beach Formation resulted mainly from reorganization, with some minor species turnover. Reorganization of species-abundance distributions that led to changes in community structure included at least four long-term, population level processes: (1) expansion and contraction in numerical dominance of the most abundant species, *Mulinia lateralis*, reflecting changes in relative environmental predictability, stability, and overall environmental rigor; (2) exchange of rank abundance levels by subdominant taxa (balanid barnacles, *Tellina texana*, *Ensis directus*, *Acteocina canaliculata*), perhaps reflecting changing importance of "equilibrium species" in successional sequences and probably changes in trophic resources; (3) promotions and demotions of numerically minor taxa, suggesting vagaries in larval recruitment patterns, changes in importance of normally sparse predatory snails, and rhythms in community complexity as reflected in species interaction patterns; and (4) continuous demotion through successively lower rank levels (*e.g.*, *Nuculana acuta*), because of gradually changing trophic resources, changing states of physico-chemical limiting factors, or de-emphasis through time of certain ecologic associations (*e.g.*, predator-prey and competitive interactions) as important elements of community structure.

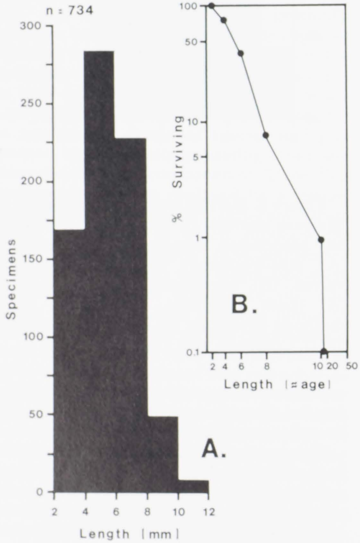

Figure 9. Normal population structure of *Mulinia lateralis* from a restricted lagoonal association (sample BC2-5, Figure 2). (A) size-frequency distribution of right valves; (B) survivorship curve based on (A).

Turnover, by comparison, mainly resulted when environmental tolerance limits of species were closely approached or exceeded, and might have been caused by alterations in salinity, temperature, turbulence, physical and chemical properties of substrates, oxygen tension, or turbidity. Species turnover may also be linked to biologic changes in the environment, involving competitive exclusion, over-predation and local eradication, amensalistic interactions, or diseases, all brought about during juxtaposition and overlapping of once geographically discrete communities during gradual changes in habitat configurations. A model of community replacement by gradual reorganization is presented in Figure 7.

Anatomy of a Single Step in the Flanner Beach Sequence. A sequence of three, vertically stacked shelly layers (minor simple shell beds) with intervening sparsely fossiliferous zones (samples BC2-3, BC2-4, BC2-5; Figure 2) straddles the transition from bay to lagoonal fossil associations. Sample BC2-4 contains a transitional fossil association with preserved compositional and structural attributes intermediate between associations at microstratigraphic levels immediately above and below it. If these minor simple shell beds represent single ecologic units or events (*i.e.*, condensed sere/pseudosere), then the detailed pattern of a step in the community replacement sequence can be analyzed by comparing the indigenous fauna of these three shelly layers.

Overall species richness declines gradually through the transition from 39 to 28 to 19 species; molluscan species richness follows a similar trend (32 to 25 to 18 species). Dominance among mollusks (Equation 1) increases gradually from 0.56 to 0.74 to 0.81; molluscan diversity (Equation 2) declines from 1.23 to 0.80 to 0.57. In descriptive trophic structure, the three samples plot close together near the infaunal corner of the substrate-niche diagram, and move gradually toward the suspension-feeding corner through the transition on the feeding behavior diagram (Figure 3).

Changes in dominance, diversity, and preserved trophic structure are largely the result of *Mulinia lateralis* becoming increasingly more important in fossil associations through the transition. The preserved population structure of *Mulinia* also changes during replacement with juvenile mortality increasing, as reflected in size-frequency distributions of valves and survivorship curves based on normal populations (Figures 8, 9). Subdominant species undergo shifts in rank position through: (1) in some cases nearly exact exchanges between two faunal components (*Acteocina canaliculata*, a gastropod, and *Abra aequalis*, an infaunal detritus-feeding clam) come very close to trading ranks between samples BC2-3 and BC2-4); (2) gradual demotion in relative abundance (*Ensis directus* from 4.2% in sample BC2-3, to 1.7% in BC2-4, then to 0.5% in BC2-5); and (3) promotion of taxa (*Nassarius trivittatus*, a vagile detritus-feeding snail, from 0.1% in sample BC2-4 to 1.7% in BC2-5). Some numerically minor species in the slightly restricted bay association completely disappear during the transition. It is important to note that certain transitions involving changes in abundance of uncommon to rare taxa may have no significance as subevolutionary changes whatsoever, but may reflect a kind of bias resulting from short-term processes (*e.g.*, localized, short-lived outbreak of predatory snails with shells disproportionately added to an attritional fossil deposit). In the overall replacement sequence, as well as in this segment of the sequence, such "false signals" are controlled by considering varied lines of evidence for long-term changes.

In this well-preserved transition step, a gradual decrease in average salinity, more complete isolation from the natural physico-chemical buffering system of open shelf waters, and slight decrease in water depth probably acted together to decrease environmental stability and predictability on the local estuarine seafloor, and to increase spatial and temporal heterogeneity of resources. Trophic supplies may have been altered. The amplitude of seasonal changes and frequency of disturbances probably increased sharply. The resident fauna reorganized at the community level through changes in species-abundance distributions, deletion of some organism populations, slight modification of trophic structure, and overall decline in number of ecologic associations and community complexity.

VI. FUTURE RESEARCH INVOLVING REPLACEMENT

Future studies of community replacement should seek to identify both the mechanisms of faunal transitions, as well as the environmental factors that propelled the changes. If replacement really is one of the main reasons for subevolutionary changes in the composition of fossil deposits in vertical sequences located between stratigraphic breaks, then many examples of this phenomenon must be available for study in rocks of many different ages with varied paleoenvironmental histories. Replacement has been happening ever since organisms became associated within communities through overlapping environmental requirements and biotic interactions, and the record of replacement in protected environments should be well-preserved for skeletalized metazoans with populations affected by habitat alteration.

It would be extremely interesting to discover the relationships and linkages between replacement, and the processes that take place during ecologic succession, community response, and community evolution. Although different from community replacement, primary succession can be viewed as the initial step in the establishment of a new community in an area after species turnover processes, associated with sharp changes in environmental settings, have eradicated all previously established resident communities (as during a regression and subsequent transgression of a continental shelf sea, or similar drastic change in habitat [see Harland, 1981; Harris *et al.*, 1984]). Transspecific evolution, on the other hand, can be pictured as occurring in the contexts of changing communities that are subject to species turnover and species-abundance reorganization in subevolutionary time (Olson, 1952; Hoffman, 1983).

Investigations of modern examples of replacement should be undertaken to understand the processes that lead to species turnover and reorganization of faunas. Modern settings in which natural habitat alteration is reshaping composition and structure of communities could be targeted for long-term sampling surveys that aim to trace the impacts of directional, long-period changes in environmental qualities. One example of a modern survey that would have an application in paleoecologic studies of backbarrier estuarine basins is the monitoring of community transitions within lagoons near short-lived tidal inlets that breach barrier islands, remain active for years to tens-of-years, then are closed or migrate. Of interest in modeling population-level mechanisms of replacement are the recent studies that involve artificial habitat alteration of diminutive ecosystems, such as small lakes and streams (Schindler *et al.*, 1985; Peterson *et al.*, 1985). But because of the long spans of time involved in development of most repalcement sequences, compared to the length of active careers of field ecologists, the study of community replacement falls more appropriately within the methodologic domain of the paleoecologist, whose business it is to evaluate fossiliferous sequences of sediments that have been compiled during thousands to millions of years.

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IX. APPENDIX
LOCALITY REGISTER

Locality numbers refer to measured sections shown in Figure 2. All fossils came from shell beds in the Beard Creek and Smith Gut members, in lower parts of bluff exposures at these localities.

BC1: Bluff, 0.6 km northwest of center of mouth of Beard Creek, at end of jeep trail about 0.3 km upstream from Whisk Point, north shore of Neuse River, southernmost Pamlico County, North Carolina; southeast corner, Upper Broad Creek 7.5' quadrangle.

BC2: Bluff, 0.3 km southeast of BC1 and 0.4 km northwest of center of mouth of Beard Creek, at Whisk Point, north shore of Neuse River, southernmost Pamlico County, North Carolina; southwest corner, Arapahoe 7.5' quadrangle.

BC3: Bluff, 0.1 km east of BC2 and 0.3 km northwest of center of mouth of Beard Creek, at Whisk Point, north shore of Neuse River, southernmost Pamlico County, North Carolina; southwest corner, Arapahoe 7.5' quadrangle.

SG1: Bluff, 3.4 km southeast of center of mouth of Beard Creek and 0.3 km northwest of Smith Gut, north shore of Neuse River, southernmost Pamlico County, North Carolina; northwest part, Cherry Point 7.5' quadrangle.

REVIEW

SEDIMENTARY AND EVOLUTIONARY CYCLES, edited by Ulf Bayer and Adolph Seilacher. Lecture Notes in Earth Sciences, 1: Published by Springer-Verlag, Berlin, Heidelberg, New York, and Tokyo, 1985, vi + 465 pp., illus., paper, $29.50

Twenty-two papers by thirty authors are presented in this volume, the printed proceedings of the symposium held at Tuebingen in September, 1983. Much of the content is concerned with the dynamics, immigration, and environmental evolution of faunas and their ecological patterns; other papers deal with dynamic stratigraphy and sea level changes.

—H.C.S.