persists, even at high internal heating rates (*11*).

Models developed from inversion of geoid, topography, and plate velocities (*12*) and from postglacial rebound studies (*13*) indicate the presence of a viscosity maximum in the mid–lower mantle. Breaks in seismic spectra are also found at a depth of 1700 km (*14*). Penetrative convection is a well-known phenomenon in fluid mechanics and is particularly associated with the minimum of the thermal expansivity of water at 4°C (*15*). In our models, penetrative convection takes place because of a local viscosity maximum. The idea of penetrative convection in the lower mantle was raised by Peltier (*16*) from linear stability analysis of mantle-like fluids with strong variations in depth-dependent physical properties. This viscosity maximum has also been predicted by asymptotic analysis (*17*). Penetrative convection emerges from the melting temperature estimates of Zerr and Boehler (*1*) in self-consistent, albeit steady-state, calculations in the highly nonlinear regime. The conditions, which are most favorable to the formation of this distinct viscosity maximum and to development of penetrative convection in Cartesian models, are a sufficiently large Ra_s (Fig. 3A), large $\Delta\eta$ (Fig. 3B), and small amounts of internal heating (Fig. 3C).

An important dynamic consequence arising from the melting temperatures of Zerr and Boehler (*1*) is the possible existence of penetrative convection in the lower mantle in situations where internal heating is low. Combined with the estimates for the depth dependence of the coefficient of thermal expansion (*18*) and the thermal diffusivity (*19*), these results would seem to suggest that the lower mantle may play only a minor role in the overall large-scale deformation of the mantle and the surface geophysical signatures, such as the geoid. Recent works (*20*) on geoid anomalies that are based on the time histories of subduction seem to support this view of a passive lower mantle that is subjected to convective forcing from the upper mantle. It is important to corroborate these findings with time-dependent calculations in order to understand better the nature of penetrative convection in the lower mantle that is caused by local viscosity maxima.

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Species Pool and Dynamics of Marine Paleocommunities

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Foraminiferal communities in the Cenozoic shelf deposits of the North American Atlantic Coastal Plain exhibit little unity during almost 55 million years of successive transgressions and regressions. Transgression communities are composed of a dynamic mixture of immigrants and newly evolved species. During regressions, species within these communities either became extinct or emigrated. Some emigrants returned during subsequent transgressions, but many did not. The neritic species of the Atlantic and Gulf continental margins constitute a species pool. Immigrants and emigrants transferred into and out of the species pool, while extinctions and originations repeatedly altered its species composition. While the results indicate a lack of local community unity, at the same time they demonstrate the necessity of a species pool to sustain species diversity.

Some ecological communities have been regarded as a kind of superorganism or unit wherein the component species are closely associated by numerous biotic interactions. Others have been considered as a group of organisms sharing ecological resources in the same time and space but acting independently of one another. Today, most ecologists share a perspective between these two extremes (*1*). Regardless of the initial viewpoint, studies of modern communities encounter difficulties in determining where the component species came from and what becomes of them when their environment ceases to exist.

The fossil record, however, does not have these constraints. The arrival and departure of species, in a given environment, can be documented over millions of years; this record constitutes a ledger, whose entries record the history of a changing community.

During a marine transgression onto a continental shelf, the newly created habitat is quickly occupied by species that are

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characteristic of the new environmental setting. Environments, such as marginal marine, inner, middle, or outer shelf, and tropical as compared with temperate, are easily recognizable by their component species and by physical-chemical attributes (*2*). When a high sea-level stand is followed by a regression, the marine species vacate the space, which is then colonized by their terrestrial coevals. Later (tens of thousands to a few million years), another transgression occurs followed by another regression. This cycle may be repeated again and again in the same geographic area. The questions that arise concern where do the species come from and where do they go and whether or not the same species, if they are still extant, reoccupy the same environment during successive transgressions—that is, whether the community behaves as a unit. In this study, we document the origination, extinction, immigration, and emigration of species in ancient, normal marine, inner to outer shelf environments in six transgressive clastic formations of the Atlantic coastal margin.

Marine onlaps and offlaps occurred repeatedly in parts of Delaware, Maryland, Virginia, and North Carolina throughout the Cenozoic (*3*). Today, the mid-Atlantic is in a partial offlap phase. The transgressive fossiliferous clastic sediments in this area of the Atlantic Coastal Plain contain a detailed record of past marine environments. We refer to the ancient seas they record as the Salisbury and Albemarle embayments (SAE) (*3, 4*). Their sediments form the Nanjemoy (lower Eocene), Piney Point (middle Eocene), Pungo River (lower to middle Miocene), Eastover (upper Miocene), and Yorktown and Chowan River (upper Pliocene) formations. These formations span nearly 55 million years of the Cenozoic.

The dynamics of shelf communities over geologic time can be inferred if that portion of the benthic community that becomes fossilized is a surrogate for the dynamics of the entire community. This requires organisms that are easily fossilized, highly diverse, abundant, widespread and, most importantly, that have a well-documented fossil record. Here we make use of the benthic foraminifera, which satisfy all of these requirements. After taxonomic standardization, 357 species were recognized in the six formations (*5*).

During the deposition of each formation, the species contained therein either immigrated into the area or evolved within it. Because a series of transgressions are being studied, those species arriving in a newly inundated area either occurred there during an earlier (except for the first) transgression into the SAE or immigrated into the basin from elsewhere. At the closure of the basins, during a regression, the species either became extinct or emigrated. In turn, the emigrating species may either have reappeared during a subsequent transgression into the SAE or may have remained elsewhere.

These possibilities were examined for each of the six formations. For example, of the 100 species recorded in the Pungo River Formation, 59 appeared for the first time and 41 immigrated (Fig. 1). Although the time span between the Piney Point and the Pungo River formations is about 24 million years (Table 1) and the average species duration of benthic foraminifera is about 20 million years (*6*), six species nevertheless occurred in both formations. In addition, six species that occurred in the Nanjemoy or Piney Point formations and were extant (five to the Recent) during subsequent transgressions never returned to the SAE. Two more species recorded in the Nanjemoy Formation never occurred in the Piney Point or Pungo River formations, but were recorded from the later Yorktown Formation.

Another 23 species, extant elsewhere during the period in which the Pungo River Formation was deposited and that appeared later in the SAE, are not present in the Pungo River Formation. In all, 31 species that were alive during the deposition of the Pungo River Formation and that occurred at some time in the SAE are not recorded in the Pungo River Formation. The sum of the immigrants (41) and the potential immigrants (31) constitutes the minimum number of available immigrants for the Pungo River formations (Fig. 1 and Table 1). Because the fossil

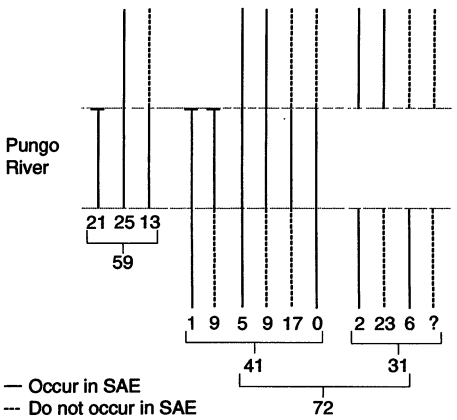

Fig. 1. All possibilities for the numbers of species extant at the time of the deposition of the Pungo River Formation. Originations (59 species) became extinct, emigrated and returned to the SAE, or emigrated elsewhere. Immigrants (41 species) originated within the SAE or elsewhere, became extinct, emigrated and returned, or emigrated elsewhere. Species (31) not recorded in the Pungo River Formation were recorded within the SAE before or after the deposition of the Pungo River Formation (or both). The question mark refers to the number of unknown species on the Atlantic and Gulf Coast continental margins that might have immigrated, but never did, into the SAE.

Table 1. Species in. Numbers of foraminiferal species pertaining to species arrivals. "Available" signifies those species immigrating into the SAE at the time of a formation's deposition plus those that were living at the same time and appearing in one or more of the other formations of this study. "Immigrate percent" is the number that immigrate divided by the number available. "Originate percent" is the number that originate divided by the total. Ma, millions of years ago.

Formation	Age (Ma)	Available	Immigrate	Originate	Total in formation
Chowan River	2.4	147	86 (58%)	6 (6%)	92
Yorktown	4–2.4	126	80 (63%)	42 (34%)	122
Eastover	8.6–6.2	112	25 (22%)	28 (53%)	53
Pungo River	18.3–10.8	72	41 (57%)	59 (59%)	100
Piney Point	44.5–42	65	34 (52%)	54 (61%)	88
Nanjemoy	57.2–52.7	41	28 (68%)	36 (56%)	64

Table 2. Species out. Numbers of foraminiferal species in categories pertaining to species departures. Percents are the number in the category divided by the total.

Formation	No. of samples	Total in formation	Emigrate return	Emigrate elsewhere	Extinct
Chowan River	9	92	54? (57%)	54? (57%)	38 (41%)
Yorktown	33	122	81 (66%)	28 (23%)	13 (11%)
Eastover	66	53	24 (45%)	13 (24%)	16 (30%)
Pungo River	115	100	39 (39%)	30 (30%)	31 (31%)
Piney Point	59	88	6 (7%)	26 (30%)	56 (64%)
Nanjemoy	72	64	12 (19%)	17 (26%)	35 (55%)

record was examined of only the 357 species that appeared at some time in the six formations, the number of species constituting potential immigrants must have been much larger. Immigration by species from outside of the SAE is clearly a dominant (35 out of 41) process. Of the 59 species that make their first appearance in the Pungo River Formation, 21 have never been recorded elsewhere and are assumed to have become extinct. Among the 41 immigrants, 10 suffered the same fate, with the result that 31 of the 100 species recorded during this interval did not survive. Twenty-five of the 59 species making their first appearance in the Pungo River Formation are recorded in subsequent transgressions of the SAE, whereas 13 emigrated elsewhere, never to return. Among the 31 surviving immigrants, 14 appeared in subsequent transgressions and 17 emigrated elsewhere. These 17 appeared in the SAE only during the deposition of the Pungo River Formation; before and after deposition of the Pungo River Formation they remain outside of the SAE. Out of the total of 69 emigrants, 39 reappear in subsequent transgressions and 30 do not. These observations are consistent for abundant, common, and rare species.

In general, the results obtained for the Pungo River Formation are similar to those obtained for the five other formations (Tables 1 and 2). Except for the Eastover Formation, about 60% of the known available species actually occupied the SAE during each transgression. This is true even though the number of available species increases, reflecting the species duration of benthic foraminifera, with time. In the Eastover Formation only 22% immigrated. Many species that emigrated from the Pungo River Formation skip the Eastover Formation and reappeared in the Yorktown Formation. The Eastover Formation is thought to have been deposited under cooler (locally and globally) and, in part, more restricted marine conditions, and this may account for some species avoiding the SAE at this time (*2*, *7*). The proportion of species originating in the SAE is highest in the four oldest formations.

The proportion of species returning to the SAE is highly variable, whereas the proportion emigrating elsewhere is about 25% (Table 2). This proportion is relatively constant regardless of the amount of time involved or climatic change. For the Chowan River Formation, 54 species survive into the modern fauna. Extinctions were greatest during the Paleogene (at the end of the Nanjemoy and Piney Point formations) and fewest at the end of the Yorktown Formation. However, 41% of the species in the Chowan River Formation, which is only slightly younger than the Yorktown Formation, do not occur in the modern fauna. This extinction is a little later than that for molluscs, which exhibit a considerable extinction (over 50%) at the top of Yorktown Formation on the Atlantic Coastal Plain (*8*).

Of the 357 species recorded in the six formations of the SAE, only 2 occur in all six, 1 in five, and 15 in four. The average species duration for neritic benthic foraminifera is about 20 million years (*6*), so the observation that only two species occur throughout all formations is not surprising. Nor is it surprising that 13 of the 15 species occurring in four formations occur in the last four.

Immigrants during a transgression are a mixture of former inhabitants of the SAE and species that were living elsewhere, mostly in neritic environments of the Atlantic and Gulf coastal plains. Similarly, emigrants, newly evolved or passing through, are composed of species that will return and those that will not. The simplest explanation of the immigrations and emigrations is that the neritic species of the Atlantic and Gulf coastal plains constitute a species pool. Dispersal for benthic foraminifera can be geologically instantaneous (*9*), with the result that most species potentially could inhabit any new embayment. However, during any particular transgression only a portion of available species inhabited the newly formed embayment. During a regression the surviving species returned to the species pool and were again available for the next transgression. Only a small nucleus of species returned habitually to the SAE. Immigrants and emigrants shuffled back and forth to the species pool while extinctions and originations continually altered its species composition.

If the species living together in these sizable embayments at any particular time are regarded as a community, then this community must be considered as a subset of a much larger community or species pool. Over geologic time, very little community unity at the species level is apparent within the SAE. Instead, the group of species (community) occupying each formation must be regarded as an ephemeral association. At the same time, the neritic benthos are an easily recognizable group and not a haphazard association of species.

Although the amount of time considered in this study is of substantially longer duration, the lack of a tightly organized community in terms of species composition is in agreement with the studies made on terrestrial communities for the Quaternary (*10*). Evidently in both the marine and terrestrial realms, many species respond to perpetually changing environments on an individual basis. To effectively do so, a species pool is necessary to supply the immigrants.

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