Reports

Species Duration and Evolution: Benthic Foraminifera on the Atlantic Continental Margin of North America

Abstract. *Average species durations were estimated for 131 commonly occurring modern species. The duration of species occurring at depths of less than 200 meters is 16 million years, while for those at greater than 200 meters and at all depths it is 25 to 26 million years. Species (less than 200 meters) distributed from Florida to Newfoundland and from Florida to Cape Hatteras have about the same durations (18 to 20 million years). The duration for species restricted to north of Cape Hatteras is only 7 million years. The data suggest that evolutionary rates are greater in shallower than in deeper depths and greatest in the shallower northern area.*

Analysis of species durations is useful for understanding the interplay of ecological and evolutionary forces (*1*). Among marine organisms the benthic foraminifera are widely distributed, and they have a well authenticated fossil record. During the Tertiary, some species living at bathyal and abyssal depths changed their depth ranges, and the specific composition of the fauna changed; but species diversity in various environments apparently remained unchanged (*2, 3*). If species diversity in a given environment remains about the same, then species duration becomes a measure of the rate of evolution.

We have recorded 876 modern benthic foraminiferal species at 542 localities on the Atlantic continental margin of North America (*4*). Most of these species occur rarely and therefore it is not possible to document their distribution in space and time with confidence (*5*). Consequently, we have chosen to examine the species durations of the more commonly occurring species. These 149 species occur at 20 (4 percent) or more localities on the Atlantic continental margin of North America.

We recorded the ranges of these species from about 7000 reports of studies, which included all the major publications on foraminifera. Realizing that many citations may be misidentifications, we compared specimens deposited in the collections of the major natural history museums of the world (*6*). The ranges used in our study are all supported by observation of many specimens. Of the original 149 selected species, 18 were discarded either because they lacked sufficient taxonomic characters to permit unequivocal identification or because specimens were observed in both the Recent and a distant geological epoch with no intermediate observations. Having designated the species ranges, we recorded the number of species observed in each epoch (*7*). The midpoint of each epoch was used to calculate the average species duration in millions of years, and species that occur only in the Recent were not used (*8*). In that all of these species are still living, these are partial ranges.

Table 1. Average species duration in millions of years (m.y.).

Category	Species (No.)	Duration (m.y.)
Entire Atlantic		
Continental margin	131	20
Less than 200 m	75	16
More than 200 m	33	26
At all depths	23	25
Florida to Newfoundland		
Less than 200 m	24	18
Florida to Cape Hatteras		
Less than 200 m	30	20
Cape Hatteras to Newfoundland		
Less than 200 m	21	7

The average species duration for the entire Atlantic continental margin of North America is 20 million years (Table 1). This is the same estimate made for deep-sea foraminifera of the Pacific (*3*), and is within the range suggested for all foraminifera (*1*) (Table 1).

On the basis of their modern distribution (*4*), we grouped the species into those that commonly occur at depths of less than 200 m, more than 200 m, and at all depths (Fig. 1). For those species that occur in shallower water the Miocene (14.5 million years ago) was a time of considerable origination. Only 7 percent of the modern fauna living in shallower water existed in the Oligocene (31 million years ago) in contrast to the deeper dwelling species and those that occur at all depths which had 24 and 30 percent, respectively. This slower evolution of deep water species was noted two decades ago (*9*).

To estimate the average duration of species in terms of their geographic distribution, we divided the fauna present in shallower water (<200 m) into (i) species that occur from Florida to Newfoundland, (ii) species that occur from Florida to Cape Hatteras, and (iii) species that occur from Cape Hatteras to Newfoundland (*10*) (Fig. 2). The species from Florida to Cape Hatteras, and from Florida to Newfoundland have similar curves and species durations (Table 1). The species from Cape Hatteras to Newfoundland, however, have a very short species duration and only 15 percent of the modern fauna extends as far back as the Pliocene.

Our calculations of durations indicate that species restricted to shallower waters, and especially northern shallow waters, have the shortest durations. Consequently, the highest rate of speciation and extinction occurs in these shallower waters. The data indicate that the rate of evolution of species capable of living in

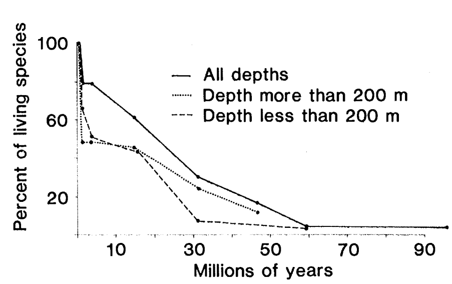

Fig. 1. The percent of living species in three depth categories plotted at the midpoint of geologic epochs.

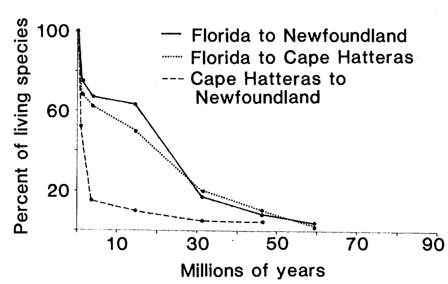

Fig. 2. The percent of living species in three geographic categories plotted at the midpoint of geologic epochs.

the more variable, shallower environments is higher than that of the species living in the deeper, supposedly more stable environments. Furthermore, the difference between species durations in shallow and deep water is far greater north of Cape Hatteras. Finally, some species are capable of living at all depths and the durations of these are similar to those of the deep water species. The data have not yet been analyzed to ascertain whether or not these species may have evolved in shallow water and then migrated to deeper water, or vice versa. Once evolved, however, these species enjoy a long duration.

Our data are difficult to compare with those obtained from work on mollusks (*11*) because of the different categories used (evidently, too few data exist on mollusk species living deeper than 200 m to estimate their species durations), but some comparisons can be made. The mollusks were divided into those species capable of living at depths of less than 1 m, and those living at greater depths, with a maximum of about 200 m. The more stenotopic deeper dwelling species are thought to have the higher rate of evolution. Species capable of living at less than 1 m (eurytopic) tolerate a wide variety of environmental conditions and are thought to be less prone to extinction and have a lower rate of evolution. The same onshore-offshore pattern was suggested for Phanerozoic shelf communities where major ecological innovations were believed to occur nearshore, but species turnover was considered higher offshore (*12*). This higher rate of evolution suggested for species living in environments with less variability is not the pattern we observe with benthic foraminifera. Instead, species restricted to the "harsher" environments have the shortest durations.

Our data indicate that the highest rate of evolution (and extinction) occurs in the more variable environments. As more data for other organisms become available perhaps their patterns of species turnover will become comparable. On the other hand, organisms may differ in their evolutionary patterns. This is certainly so when we consider the average species duration which, regardless of the environment, is two to three times longer for benthic foraminifera than for mollusks.

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Ionospheric Sporadic-E Parameters: Long-Term Trends

Abstract. *The results of observations over 3½ solar cycles of ionosonde parameters describing sporadic-E patches (E_s) are given for two Southern Hemisphere stations. Analysis has revealed systematic changes in the occurrence probabilities of f_oE_s and f_bE_s, changes that are independent of time of day or season. It is unlikely that observational effects can be entirely responsible for the trends, which suggest that major long-term changes may be occurring at E region heights.*

The ionospheric E region, produced by the photoionization of O_2 by solar continuum, Lyman β, and electron precipitation, extends from 100 to 130 km and contains plasma irregularities of various scales. One manifestation of the irregular nature of the region is the presence of localized patches of enhanced ionization some 300 km in horizontal scale and 1 to 3 km in vertical extent which occur in quasi-random fashion within the normal E region and have individual lifetimes of about 1.5 hours. These sporadic-E patches (E_s) are formed by the action of tides in the neutral atmosphere, bringing about the compression of electrons and positive metallic meteoric ions into thin sheets (*1*). The action of tidal winds is modified by internal gravity waves and turbulence, producing the essentially sporadic feature of this enhanced ionization. The morphology of E_s, the mechanisms controlling its formation, and its aeronomy are not well understood.

An international network of vertical swept-frequency radars (ionosondes) has been operating for decades, providing ionospheric data. The published hourly values of E_s parameters available from scaled ionograms are the ordinary wavetop penetration frequency (f_oE_s) and the highest frequency for which blanketing occurs for layers at greater altitudes (f_bE_s). In order to understand the aeronomy of E_s, it is necessary to relate the E_s parameters to identifiable properties of E_s patches. Although such relations are not clearly defined, it is known that f_bE_s is a measure of the ambient ionization density in an E_s cloud whereas f_oE_s is thought to be determined by the density of ionization irregularities within a cloud. Although hourly sampling at one ionosonde cannot yield detailed information about individual clouds, a long series of such ionosonde data is valuable in providing information on overall temporal characteristics. Thus, it is well known that temperate-latitude E_s is a daytime summer phenomenon (*2*) with daytime f_bE_s showing an in-phase solar cycle correlation (*3*).

Since reports of long sequences of E_s data are sparse, it is of interest to note that the New Zealand Department of Scientific and Industrial Research has provided scaled E_s parameters since 1947 for its network of ionosonde stations in the South Pacific. In an effort to determine the long-term characteristics of E_s occurrence, I have examined f_oE_s and f_bE_s values for two stations: Rarotonga (21.2°S, 200.3°E) in the subtropical region and Christchurch (43.5°S, 172.5°E) in the temperate zone. The mean monthly occurrence probabilities, *P*, were determined for three separate