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On the Relationship between Species Distribution-Abundance-Occurrence and Species Duration

MARTIN A. BUZAS[a*] and STEPHEN J. CULVER[b]

[a]*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560–0121, USA and*
[b]*Department of Geology, East Carolina University, Greenville, North Carolina 27858, USA*

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Most abundant species are also geographically widely distributed. Widespread species are likely to occur at more sampling localities than narrowly distributed species. In addition, a few studies indicate that widely distributed species have longer species durations. Here, we test the validity of these generalizations for benthic foraminifera. Data from samples representing time slices spanning 57 My of the Cenozoic, from the North American Atlantic Coastal Plain, were used. Modern distributions of species surviving from these time slices and now living on the continental margins of North America were also used. The analyses confirm a positive statistical relationship linking geographic distribution, abundance, and frequency of occurrence. However, regression of species durations against frequency of occurrences, as well as against the abundance of individuals occurring in each time slice, indicated almost no relationship. Furthermore, for species surviving in the modern fauna, neither a regression comparing species durations with frequency of occurrence nor a comparison of species durations with geographic spread around North America was significant. Our data suggest an initial, trial period of "establishment" extending up to 2 or 3 My for originating species. In contrast to most earlier studies, we find that the likelihood of extinction of species which survive this initial interval is the same, regardless of their distribution-abundance-occurrence.

Keywords: Distribution, abundance, occurrence, duration, foraminifera

INTRODUCTION

Consider an area with many sampling localities. If a single individual were found representing a species at a single locality, the species would be regarded as rare and its distribution narrow. A single individual can necessarily occur only at one locality; this is defined as one occurrence. Species represented by two individuals could occur either at one locality or two. Species represented by many individuals might be found at one, two, three, … all localities. In the last case, the number of individuals must equal or exceed the number of localities, and the number of occurrences equals the number of localities. Clearly, when a species occurs at all localities, the number of individuals representing this species might be orders of magnitude greater than the number of localities, but the number of occurrences cannot exceed the number of localities. A species represented by many individuals and found at all localities would be regarded as abundant and its geographic distribution as widespread. Notice that a rare species, repre-

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* Corresponding author: e-mail: buzas.marty@nmnh.si.edu

sented by one individual, must necessarily have a narrow distribution, but an abundant species might have either a narrow or a widespread distribution. One can imagine a situation where a single individual of a particular species is observed and counted at each of the sampling localities (widespread distribution), while an abundant species represented by far more individuals than the number of sampling localities occurs at only one locality (narrow distribution).

The relationship between abundance and geographic spread or range of distribution has been examined for a wide variety of organisms. A significant positive statistical relationship is well established (Hanski, 1982; Brown, 1984; Gaston, 1996; Rosenzweig, 1995; Watts *et al.*, 1998). From a statistical point of view, it is unlikely that an abundant species will occur at only one or a few localities. Instead, numerically abundant species most often occur at many localities and are geographically widespread, while the less abundant species occur at fewer localities and are more narrowly distributed. Given these relationships, we might also expect a positive correlation to exist between abundance and occurrence. Such a correlation has also been demonstrated, for a wide variety of organisms by Brown (1984), and for foraminifera by Hayek and Buzas (1997). We have evidence, then, of positive statistical relationships linking distribution, abundance and occurrence. This conjunction will be further substantiated by the results presented here.

Logically, at any particular time, species with wide geographic ranges are more likely to survive a localized catastrophe than those species that are restricted to the site of the disaster. Therefore, a positive relationship between geographic range and species duration or longevity might be expected. Such a positive relationship has been found in some studies (Hansen, 1978; Jablonski *et al.*, 1985; Jablonski, 1987; but see Stanley, 1986, 1990). The positive correlation between geographic range and duration is so plausible as to seem self-evident, and it is widely accepted as an established fact (Rosenzweig, 1995). Here, we examine the relationships of species abundance, frequency of occurrence, and geographic range with the durations of species of benthic foraminifera, one of the most widely distributed groups of marine organisms, in space and time. To do so, we investigate these relationships in Cenozoic paleocommunities from five stratigraphic units, as well as in the distributions of survivors from these times that are living in present-day seas, around North America.

TIME SLICES REPRESENTED IN THE SALISBURY AND ALBEMARLE EMBAYMENTS

Sediments extending across parts of Delaware, Maryland, Virginia, and North Carolina accumulated in what are known as the Salisbury and Albemarle embayments (SAE). This area was subjected to marine transgressions and regressions, repeatedly throughout the Cenozoic. The benthic foraminifera from clastic sediments deposited when the SAE was flooded indicate normal marine environments of the inner to outer shelf (Buzas and Culver, 1994, 1998). We use data from six formations: Nanjemoy, 57.2–52.7 Ma, $n = 72$ samples, $S = 64$ species; Piney Point, 44.5–42.0 Ma, $n = 59$, $S = 88$; Pungo River, 18.3–10.8 Ma, $n = 115$, $S = 100$; Eastover, 8.6–6.2 Ma, $n = 66$, $S = 66$; Yorktown, 4.5–3.0 Ma $n = 33$, $S = 122$; and Chowan River, 2.5–1.9 Ma, $n = 9$, $S = 92$. These six formations are taken to represent five time slices or intervals. Four time slices are recorded by single formations. One interval (Yorktown-Chowan River, 4.5–1.9 Ma, $n = 42$, $S = 132$) is represented by two formations that are considered together on account of the similarity of their faunas and the small amount of time that elapsed between them (Buzas and Culver, 1998). Our data from the five time slices is based on 354 samples, from which 66,002 specimens belonging to 356 species of foraminifera were extracted (Buzas and Culver, 1998).

TEMPORAL COMPONENTS OF FAUNAS WITHIN TIME SLICES

The number of species found within each of the fossil assemblages in each of the time slices can be divided into four temporal components (Buzas and Culver, 1994): (1) species with a previous fossil record and a subsequent fossil record, immigrating-emigrating = IE; (2) species with a previous fossil record and no subsequent fossil record, immigrating-extinct = IX; (3) species originating during the time slice which also have a subsequent fossil record, originating-emigrating = OE; (4) species originating during the time slice which have no subsequent fossil record, originating-extinct = OX. The total number of species within each time slice is: S = IE + IX + OE + OX (Figure 1). A balanced situation exists when the number of immigrants (I = IE + IX) equals the number of emigrants (E = IE + OE). In this case, when I = E, then we always have IX = OE. Notice also that the OX category makes no contribution to the relation between immigrants and emigrants; OX is not included in either of the equations for I and E, although it is an integral part of the expression for S. Species in the OX category were called "loopers" for this reason by Buzas and Culver (1998).

The foraminifera have been studied extensively. Placement of each species in the categories defined above and their longevities in geologic time were based on a worldwide search to establish the fossil distribution of each species. The geologic ages of the species were determined by referring to 142 well-dated formations, most of which occur on North American coastal plains adjacent to the Atlantic and the Gulf of Mexico (Buzas and Culver, 1998).

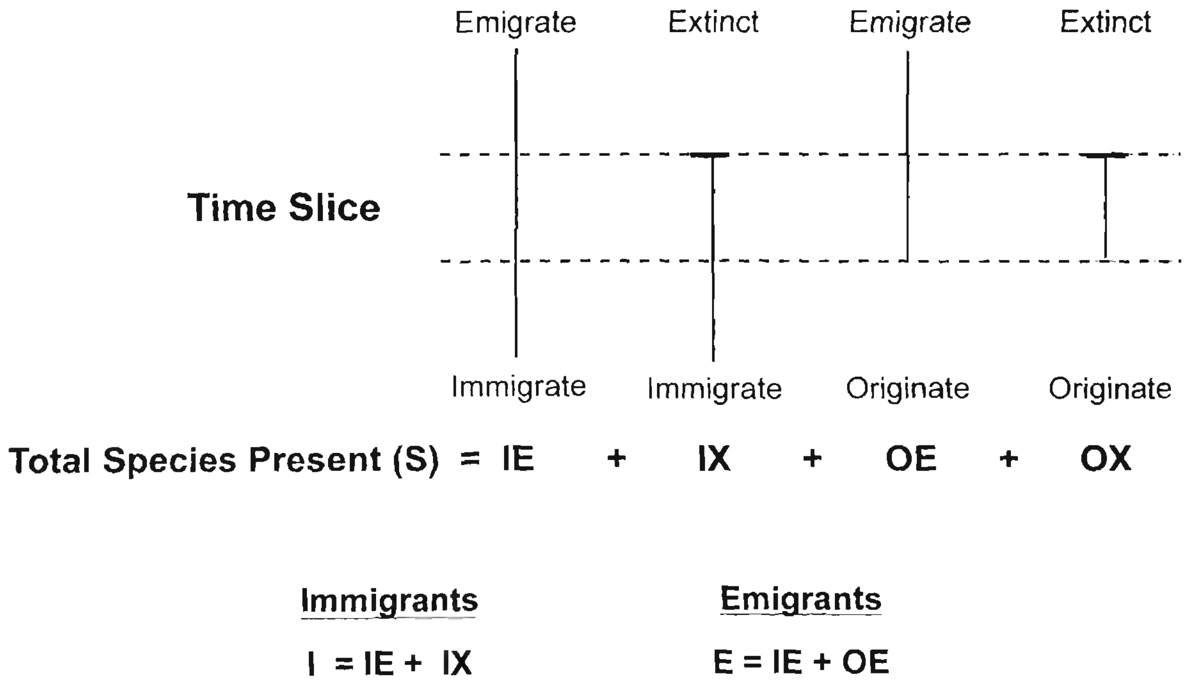

FIGURE 1 Species in four temporal components (categories) occurring within a time slice. Vertical lines indicate geologic ranges. A horizontal bar terminating a range indicates extinction

STATISTICAL ANALYSES OF DATA BY TIME SLICE

Regressions were calculated on data from each of the time slices. The dependent variable for all the regressions is species duration, as determined from our world-wide search. For the Paleogene time slices (Nanjemoy and Piney Point), most durations are complete because most of the species are extinct. Only four species (6%) from the Nanjemoy and eight (9%) from the Piney Point are extant. For the Neogene, in the Pungo River 49 (49%) of the species are extant and in the Yorktown-Chowan River 79 (60%) are extant. The mean species duration for all 356 species in the SAE is about 15 My.

Species in the OX group necessarily have short durations. Because these species have truncated longevities, it is more meaningful, statistically and biologically, to exclude this group of 147 species from the analysis. The mean duration for the remaining 209 non-OX SAE species is 21 My. The mean duration for 120 non-OX extinct SAE species is 18 My and the mean partial (incomplete) duration for the 89 extant species is 25 My. These estimates, excluding the OX species, compare favorably with the estimate of 21 My for the mean partial durations of 267 extant species inhabiting the North American Atlantic continental margin (Buzas and Culver, 1989) and the 21 My estimate for 128 extant species from New Zealand (Hayward *et al.*, 1999). Thus, with the OX group excluded, estimates of mean species duration are similar whether partial or only complete longevities are taken into account.

Regressions were run using both occurrences and numbers of individuals as the independent variable. For example, from the Nanjemoy there were 72 samples which yielded 64 species. The two most numerically abundant species occurred in all 72 samples; the rarest, nine species in all, each occurred in only one sample. The total number of individuals of the most abundant species, in all 72 samples, was 2328; for the rarest species it was equal to one. As might be expected, a regression with occurrences as the dependent variable and the total number of individuals as the independent variable, with a sample size of 64 species as the number of observations, is statistically significant ($p < 0.001$ with $r^2 = 0.70$). Similar regressions comparing frequency of occurrence with total numbers of individuals for each time slice were all significant, with $p < 0.001$ and r^2 averaging 0.49, confirming results for modern foraminifera from the Gulf of Mexico obtained by Hayek and Buzas (1997). These results suggest that regressions taking either numbers of individuals or occurrences as the independent variable would be sufficient. Nevertheless, for each time slice, we ran regressions of species duration against occurrences as well as individuals, always obtaining equivalent results.

Given these considerations and the fact that only occurrences are available for the modern data, which we will introduce later, all the analyses reported here are based on occurrences as the independent variable (Figure 2). For each time slice, an initial regression was computed including species from all four temporal components. A second regression was run with the OX component removed because, as we have already indicated, these species have necessarily limited durations and also fewer occurrences. Finally, a third regression was run with both the OX and OE components removed leaving only the $I = IE + IX$ species. If a time slice is considered as a former "modern" time plane, these are the only species which would at that time have had a fossil record. So, this third regression is comparable to an analysis of a modern fauna, where partial durations are known for species with fossil records.

When all the temporal components are included, two of the regressions (Figure 2B, 2D) are significant ($p < 0.05$). When OX is excluded only one (Figure 2D) remains significant. When OX and OE are excluded, all are non-significant. The OX species not only have truncated durations, but they also exhibit fewer occurrences

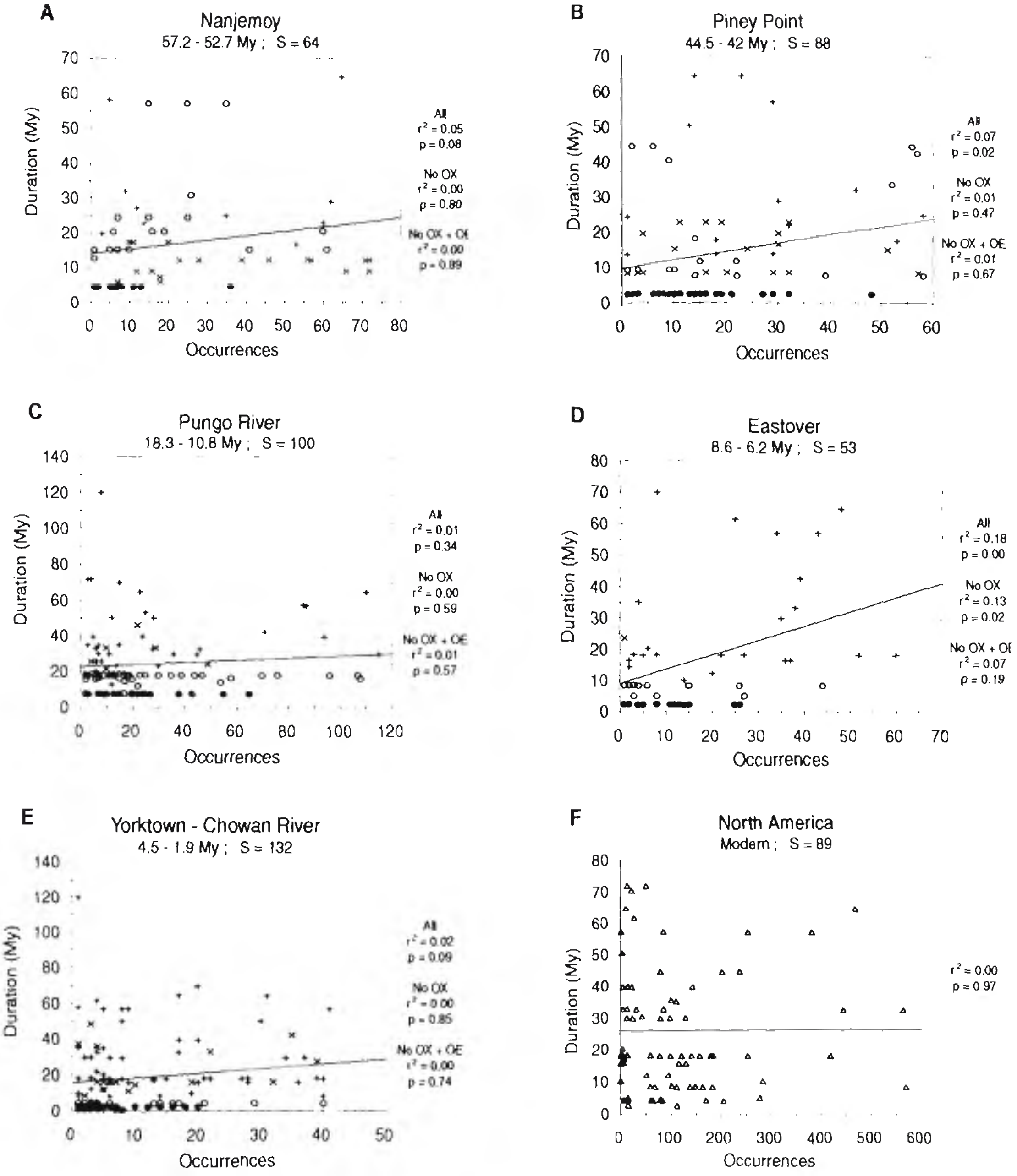

FIGURE 2 Regressions of species durations against their frequencies of occurrence for five time slices (A-E) and for the modern seas around North America (F). Note different scales. For time slices based on fossil faunas: +, species with previous and subsequent fossil records, immigrant-emigrant (IE); X, species with a previous fossil record and no subsequent fossil record, immigrant-extinct (IX); O, species with no previous fossil record and a subsequent fossil record, originating-emigrant (OE); •, species with no previous or subsequent fossil record, originating-extinct (OX). For modern North American fauna: Δ, species with a fossil record, surviving from the past into the modern time slice, I = IX + IE. Regression lines are drawn for analyses of all species. S = number of species, p = probability associated with F-value for each regression

than species in the other categories (Figure 2A-2E). The OE category exhibits progressively shorter durations over time (toward the present) while the IE category exhibits longer ones (Figure 2A-2E). The OE species from the Paleogene (Figure 2A, 2B) are not constricted by time like those of the Neogene whose origins are closer to the present. Note also that some (not all species remained in the SAE) of the OE species from earlier time slices become members of the IE components of later time slices. The IX species in the Paleogene (Figure 2A, 2B) have a shorter duration than the IX species in the Neogene (Figure 2C-2E). This occurs because most immigrants into the Paleogene time slices originated in the Paleocene. Thus, although the time slices span 57 My, truncation of species ranges at both ends is evident.

These data also show that species in the IX category become extinct regardless of their numbers of occurrences and total abundance (Figure 2A-2E). Consequently, the likelihood of extinction is the same, regardless of abundance and frequency of occurrence. In Figure 2C and 2D, the numbers of species in the OE category far outnumber those in the IX category, indicating the pulse of diversification that contributed greatly to the modern day species richness (Buzas and Culver, 1989, 1991).

STATISTICAL ANALYSES OF MODERN FORAMINIFERA

Culver and Buzas (1980, 1981, 1982, 1985, 1986, 1987) have documented the distribution of modern benthic foraminifera around the continental margins of North America. This data set consists of 61,369 occurrences of 2,329 species from 2,673 localities, distributed in the Arctic, Atlantic, Pacific, Gulf of Mexico and Caribbean. Of the species that lived in the SAE during the Cenozoic, 89 still occur (all I in the modern fauna) around North America today. Our analyses for the time slices discussed above were confined to data from an area comprising only part of the Atlantic continental margin, that is the SAE. The analysis of distributions of the 89 survivors covers a much larger area, namely the entire continental margin of North America, including the Caribbean. A regression analysis comparing partial species durations against occurrences for these 89 species is not significant (Figure 2F).

To further examine the relationship of species duration with geographic range, we subjected the data to an analysis of variance. Species were grouped in classes according to their occurrence in 1, 2, 3, 4 or 5 of the Arctic, Pacific, Atlantic, Gulf of Mexico, and Caribbean regions. Species occurring in only one of these regions can be regarded as endemic, while those occurring in five regions are ubiquitous or cosmopolitan. Analysis of variance of species durations indicates no significant difference in mean duration among the five categories ($F_{4,84} = 0.99$, $p = 0.42$), confirming the lack of a relationship between species duration and geographic range (Figure 3A). Further analysis confirms the relationship between geographic spread or distribution and the number of occurrences. Analysis of variance of the number of occurrences in the five regions is significant, $F_{4,84} = 13.31$, $p < 0.001$ (Figure 3B). In other words, species having the greatest geographic spread also have the highest number of occurrences. This confirms the relationship among geographic spread (distribution), number of individuals (abundance), and frequency of occurrences.

Analyses of data from the time slices considered here are all from one geographic region, the Salisbury and Albemarle embayments of the Atlantic coastal plain. Species that occur frequently during a time slice in the SAE may not occur frequently elsewhere. Similarly species that occur rarely in the SAE may occur frequently elsewhere. We have no way of determining the extent to which these patterns occur in the fossil record. However, the modern data set allows us to do so. Examination of data from around the continental margins of North Amer-

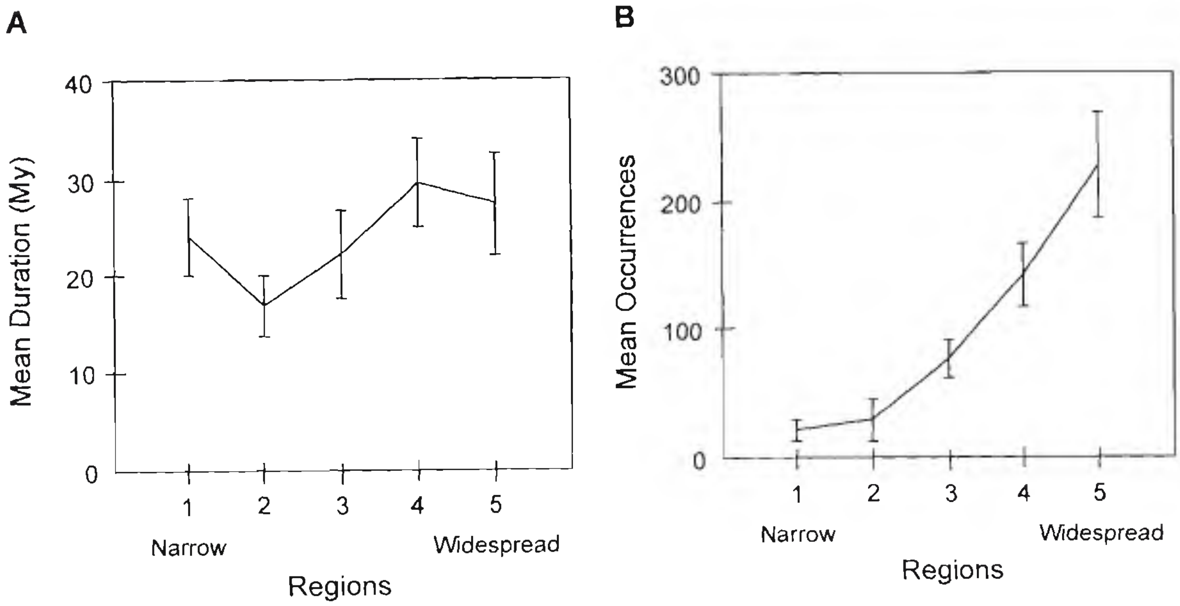

FIGURE 3 (A) Mean species durations compared with geographic ranges of 89 foraminiferal species of the Salisbury and Albemarle embayments surviving in the modern fauna. The differences in mean species duration among regions are not significant. (B) Mean number of occurrences compared with modern geographic ranges of 89 surviving species of the SAE. The differences in mean numbers of occurrences among regions are significant. The continental margins of North America were grouped into five regions: Arctic, Atlantic, Pacific, Gulf of Mexico and Caribbean. The plot groups species that are present in 1, 2, 3, 4, or 5 regions

ica confirms that species which occur frequently on the Atlantic margin may not occur frequently elsewhere. On the other hand, species that occur rarely on the Atlantic margin may occur frequently elsewhere, and some species, usually rare, maintain about the same number of occurrences everywhere. The question then, is whether or not these changes offset one another, so that an analysis based on one region is applicable to the whole. To test this hypothesis, we ran a regression comparing species durations against frequency of occurrences for the 62 surviving species from the SAE that currently inhabit the Atlantic continental margin of North America. The results are nearly identical to those obtained when all five regions were tested. The ANOVA on this regression has $p = 0.89$ while $r^2 = 0.00$ (compare with Figure 2F).

SIGNIFICANCE OF THE OX TEMPORAL COMPONENT

These analyses and visual inspection of Figure 2 indicate little relationship between the duration of benthic foraminiferal species and their abundance, frequency of occurrence and geographic ranges. However, the OX category of species with short durations clearly has fewer occurrences. Perhaps the survival of newly originating species is related to the number of occurrences. We subjected the mean numbers of occurrences in the OX and OE categories for each time slice to an analysis of variance. In all cases, the mean number of occurrences is less for the OX than for the OE category of species and significantly so in all cases except the Pungo River (Figure 2C) and the Eastover (Figure 2D) time intervals.

The Yorktown-Chowan River couplet offers a further opportunity to examine the relationship of newly originating species to their frequencies of occurrence. In the Yorktown Formation (4.5–3.0 Ma), 9 species are OX and 34 species are OE (Buzas and Culver, 1998). These 34 OE species appear as immigrants in the Chowan River Formation (2.5–1.9 Ma), during which time 20 species became extinct and 14 species survived into the modern fauna. So, we have species that are confined to the Yorktown (9 species, duration 1.5 My), species appearing in the Yorktown and Chowan River (20 species, 2.6 My) and species ranging from the Yorktown to the present day (14 species, 4.5 My). Analysis of variance on the mean number of occurrences in these three groups is significant ($F_{2,40} = 3.37$, $p = 0.04$), and a contrast of data for the Yorktown to modern species against the other two groups is significant ($F_{1,40} = 6.71$, $p = 0.01$). There is no significant difference in mean frequency of occurrences between species confined to the Yorktown and those of the Yorktown-Chowan River ($F_{1,40} = 0.16$, $p = 0.69$). The same results were obtained when individuals were used instead of frequency of occurrences. These results suggest that survival up to two or three million years (2.6 My in this particular instance) may depend, for some species, on their frequencies of occurrence. Once species survive this trial period of "establishment", no relationship between species duration and frequency of occurrences is evident (Figure 2F). The decomposition of species data for each time slice into separate components strengthens the analyses. The inclusion of OX species in an analysis artificially strengthens the apparent relationship, so these species should be eliminated from studies where the supposed link between species duration and geographic distribution is being assessed. Note that in Figure 2A-E the value of r^2 is always larger when the OX component is included.

DISCUSSION

Benthic foraminifera reproduce both asexually and sexually, often several times a year (Lee and Anderson, 1991). Great numbers of juveniles and/or free-swimming gametes are produced. Combined with the ease of transport of such small organisms, this leads to a high dispersal capability (Buzas and Culver, 1991). The immense fecundity of these organisms results in extremely high densities of living individuals, which often reach several hundred in a few milliliters of sediment (Wefer and Lutze, 1978; Buzas, 1978). Thus, a few km^2 of seafloor may be populated by many millions of individuals. Even "rare" species, represented by one or a few specimens in samples from a few cm^2 may represent populations of more than 10^{10} individuals over a few km^2. Consequently, even if species with relatively few occurrences are geographically restricted, their vast numbers would mitigate against extinction (Johnson, 1998; Gaston, 1998). This is consistent with the evidence presented by Stanley (1986), who showed for small, burrowing, siphonate bivalves that the effect of numerical abundance, which is inversely correlated with body size, overwhelms geographic range as a factor in their survival. Here, we have demonstrated a significant, positive statistical relationship linking range of geographic distribution, abundance, and frequency of occurrence of benthic foraminifera, but species duration is not related to these variables. Abundant species are as likely to become extinct as rare species (Buzas and Culver, 1998) and widely distributed species with many occurrences do not have significantly longer durations (Figure 3A). Perhaps in large-bodied, less numerically abundant species, the population densities of rare species are sufficiently low that their probabilities of extinction are high relative to those of abundant species. If large-bodied organisms exhibit a positive relationship between their ranges of geographic distribution and abundance, like the foraminifera studied here, the relative importance of geographic range and abundance (population density) in determining species duration will be difficult to assess.

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