Diversity of Planktonic Foraminifera in Deep-Sea Sediments

Abstract. *The diversity of a planktonic foraminiferal assemblage on the ocean floor depends on the state of preservation of that assemblage. As dissolution progresses, species diversity (number of species in the assemblage) decreases, but compound diversity (based on relative species abundance) first increases and then decreases; species dominance first decreases and then increases. The reason for these changes is that the species most susceptible to solution deliver more sediment to the ocean floor than do species with solution-resistant shells, possibly because the more soluble tests are produced in surface waters, where growth and production are greatest.*

Ecologic extrapolations from living creatures to their fossil ancestors of the remote past are unreliable, and therefore many paleoecologists have turned their attention to information that is independent of particular taxa, such as the functional morphology of fossils and the diversity of entire assemblages (*1, 2*). Because planktonic foraminiferal remains are widely distributed on the deep-sea floor, their diversity patterns are especially valuable in the reconstruction of latitude positions and circulation patterns of past ages (*3, 4*). In studying foraminiferal sediment assemblages, or indeed any fossil assemblages (*5*), it must be remembered that differential production (*6*) governs the transition from life to death assemblages and that differential dissolution (*7, 8*) and other processes alter the death assemblages to form the sediment assemblages.

Here we present evidence to show that differential dissolution of planktonic Foraminifera influences the diversity patterns on the ocean floor in a characteristic way. Our data are taken from a study of foraminiferal distributions in South Pacific sediments (*9*).

Many indices are available for measuring diversity (*10*). Some depend on the observation that the number of species (S) found in any one sample tends to be proportional to the logarithm of the number of specimens (N) counted ($D_L \sim S/\log N$), some are based on probability theory, and others are arbitrary. All are functions of the number of species present, their relative abundances, or both. For the present analysis we chose four indices that are frequently used.

The species diversity is simply the number of species found in a sample:

$$D_S = S \qquad (1)$$

In our samples, 2000 to 3000 specimens were scanned to obtain S; thus, log N is nearly constant and D_S is almost directly proportional to D_L. Without the precaution of scanning large numbers of specimens, the species diversity becomes rather dependent on sample size. This dependence must be considered, especially when combining counts from various sources, as has been done previously (*4*).

The species dominance is given as

$$D_D = p_{\max} \qquad (2)$$

where $p_{\max}$ is the maximum proportion of any one species in a sample. The dominance is the simplest of the indices that make use of species proportions to define diversity. Two other indices making use of species proportions are considered: a modification of Simpson's index and the Shannon function. These two indices depend on the whole spectrum of species proportions and are here referred to as "compound diversity."

Simpson's index (*11*) can be rewritten as

$$D_P = 1 - \sum_1^S p_i^2 \qquad (3)$$

in which form it measures the probability that two specimens, picked at random from a sample of infinite size, belong to different species. This probability may be taken as a measure of diversity of an assemblage.

The Shannon function

$$D_H = -\sum_1^S p_i \ln p_i \qquad (4)$$

is a measure of the information necessary to specify an assemblage (*2*).

The various indices are interrelated (Fig. 1). Species diversity and compound diversity are only moderately well correlated (Fig. 1, A and C), whereas a good correlation exists between dominance and compound diversity. Once the proportion of the most abundant species in a sample is

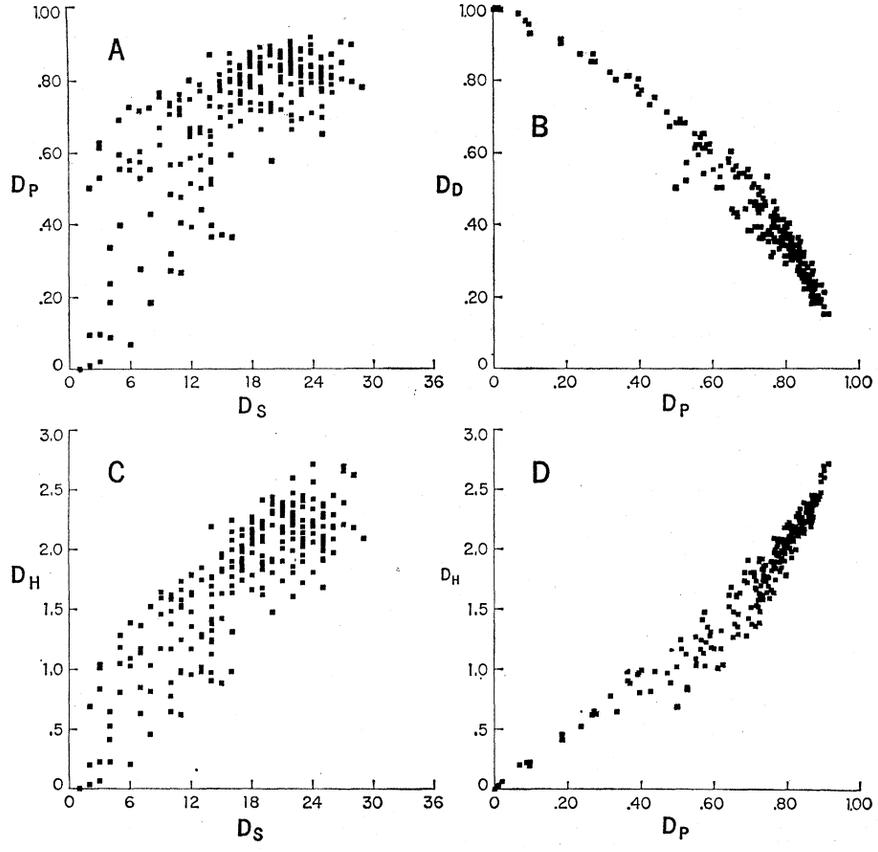

Fig. 1. Relationship between various diversity indices in planktonic foraminiferal assemblages from South Pacific surface sediments. D_P, D_S, D_D, and D_H are defined in text.

specified, the range of the measures of compound diversity, notably of D_P, is rather narrowly circumscribed. No biological significance can be assigned to such regularities that arise from definitions. In our samples such interpretations would be unwarranted in any case, since the present sediment assemblages result both from biological processes in the upper waters of the ocean and from chemical dissolution on the deep-sea floor.

This twofold influence becomes obvious when the diversity of each sample is plotted against its latitude and against its state of preservation (Fig. 2). The dependence of D_P on latitude is not well defined (Fig. 2B); hence, we may expect latitudinal trends of D_H and of D_D to be similarly poorly developed. The large scatter precludes any generalizations beyond the observation that maximum values of compound diversity become distinctly lower in high latitudes, owing to the well-known dominance of *Globigerina pachyderma* in subpolar regions. The maximum values of the species diversity (D_S) tend to decrease from tropical to antarctic latitudes in a somewhat more orderly fashion than do values of compound diversity (Fig. 2A). A curious minimum appears, however, in the vicinity of the equator. The general trend of maximum D_S values reflects the latitudinal diversity pattern noted by Murray (*12*). The trend is evident in charts of species range (*13*) and is useful for paleoecologic reconstruction (*3*, *4*). The equatorial anomaly and the pronounced scatter of D_S largely reflect differential preservation.

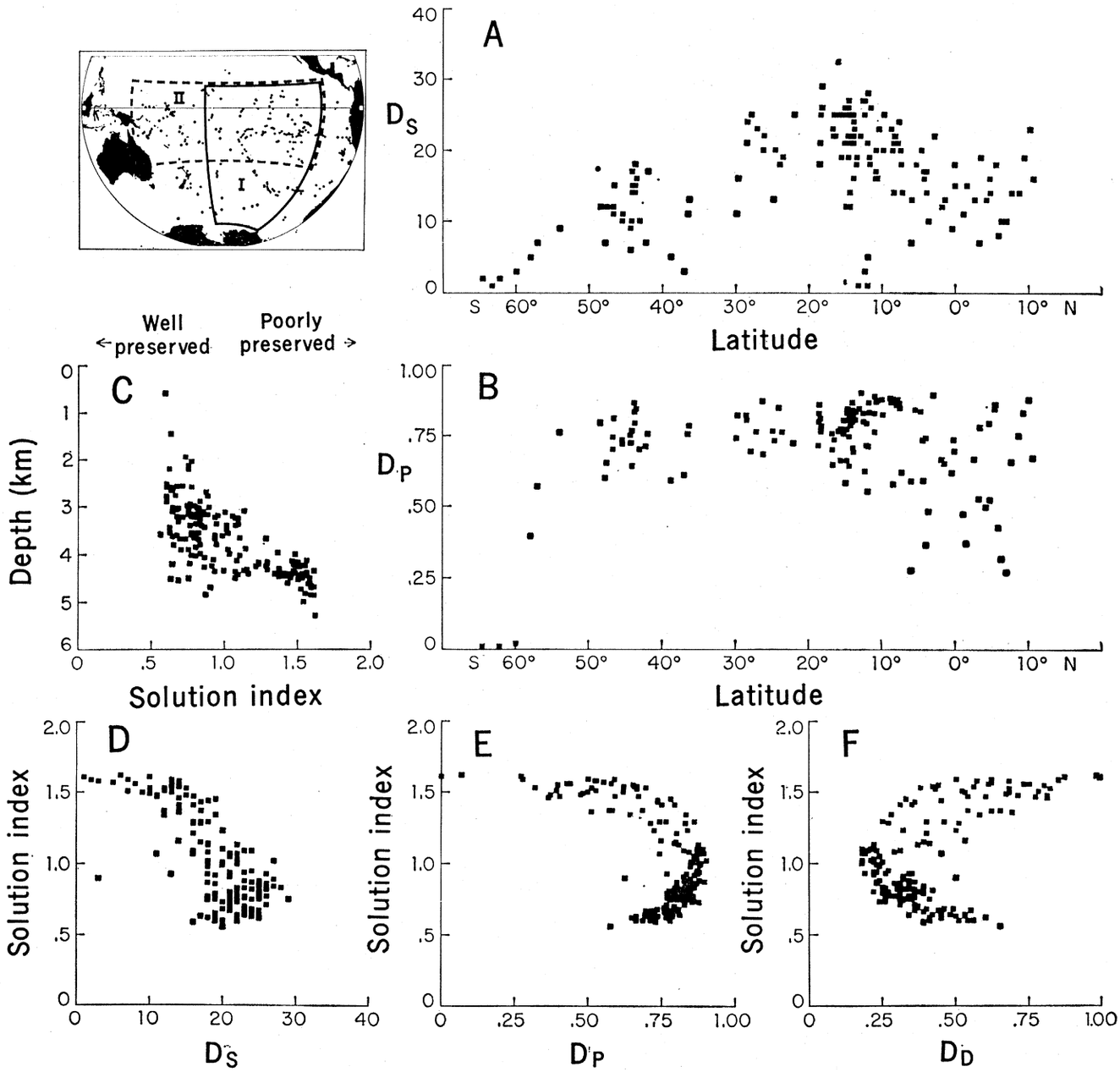

Fig. 2. Dependence of diversity indices of planktonic foraminiferal sediment assemblages on latitude and on state of preservation. (A, B) Based on sample in area I (inset). (C, D, E, F) Based on samples in area II (tropical region only). Solution indices are calculated by using a rank list of all species, in which the Foraminifera are ordered in sequence of their solubility (*8*). The index is the average rank of a sample, divided by a constant (the overall median rank). High solution indices denote poor preservation.

The depth profile of foraminiferal samples according to their states of preservation (Fig. 2C) suggests that in the tropical region there is a zone between depths of 3 and 4 km below which foraminiferal shells dissolve markedly (*14*). The occurrence of well-preserved samples below this zone is believed to reflect postdepositional displacement of sediments. A similar level of change in preservation ("lysocline"), has been found in the central Atlantic at somewhat greater depth (*8*). In the Pacific, this lysocline appears to coincide with a drastic change in the rate of calcite solution in the water column, as found by experiment (*15*). The lysocline is less distinct and relatively shallow in fertile areas, probably owing to the large amount of organic carbon and the concomitant carbon dioxide production in the sediment (*8*). Thus, dissolution of Foraminifera appears more pronounced in the fertile equatorial areas than in adjacent tropical regions (*9*), which accounts for the equatorial minimum in species diversity on the ocean floor.

If some species dissolve faster than others, it is immediately clear why dissolution decreases the number of species encountered in a sample (Fig. 2D). The occurrence of maximum values of compound diversity in assemblages at intermediate stages of preservation, with corresponding minimum values of dominance (Fig. 2, E and F), needs some comment, however.

In tropical areas, low diversities occur in samples that are well preserved, where *Globigerinoides ruber*, *Globigerinita glutinata*, and, to some extent, *Globigerinoides sacculifer* dominate because of their high shell output. Low diversities also occur in poorly preserved samples, where *Globorotalia tumida*, *Pulleniatina obliquiloculata*, and *Globoquadrina dutertrei* dominate because of their great resistance to dissolution. These resistant species are relatively rare in well-preserved samples. The compound diversity maximum at intermediate stages of dissolution is, therefore, contingent on the fact that species with high shell output tend to dissolve easily, so that, upon dissolution, dominance first decreases, as the abundant species are removed, and then increases again as certain resistant species begin to dominate the assemblage (*16*). Contouring of dominance patterns without regard to this mechanism (*4*) is likely to lead to unwarranted conclusions when such patterns are related only to biological processes in surface waters.

Why should the initially dominant species of the tropics dissolve most rapidly? These highly productive species live in surface water (*17*) and build relatively light, open-structured, porous shells, possibly in response to rapid growth or to the low viscosity of warm surface waters, or to both, and these thin shells are able to stay in the euphotic zone. On the other hand, living representatives of resistant species of the more common thick-shelled types encountered in sediment assemblages tend to live below the photic zone (*18*), where growth is slow and may manifest itself chiefly as an increase in shell thickness and density (*19*). Thus, the previously noted correlation between depth distribution and solution ranking (*8*) is not a coincidence. This correlation is the cause of the observed compound diversity maximum (and dominance minimum) in foraminiferal assemblages showing intermediate preservation. Such assemblages tend to occur near the lysocline.

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Morphine: Radioimmunoassay

Abstract. *The development of a radioimmunoassay for morphine is described. The hapten morphine is made antigenic by coupling it to a protein at the phenolic group of the molecule. Extremely low concentrations of morphine (0.5 nanogram) can be measured by this assay procedure.*

Despite the fact that extraction procedures and thin-layer chromatographic methods for assaying morphine have been used successfully (*1*), these techniques are relatively time-consuming, laborious, and lack sensitivity with respect to analysis of unlabeled morphine. We now describe procedures for the conjugation of morphine to protein, and for the radioimmunoprecipitation of this conjugate with specific antiserum, which can be used to measure nanogram amounts of morphine in serum.

Morphine was converted to 3-*O*-carboxymethylmorphine by reaction of the free base with sodium-β-chloroacetate in absolute ethanol (*2*, *3*). The product after recrystallization from hot absolute ethanol had a melting point of 292° to 293°C. The 3-*O*-carboxymethylmorphine acid was positive by the Dragendorff test and negative by the Pauly test (*4*) and had an R_F of 0.6 on thin-layer silica-gel chromatography, with glacial acetic acid and methanol (1:1) as the solvent system. In the same solvent system