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RESEARCH STRATEGY IN PALEOSYNECOLOGY OF MARINE BENTHOS

Strategia badawcza w paleosynekologii morskiego bentosu

Abstract. Evolutionary-ecological models relating the process of speciation and species extinction to a framework delimited by the structure of ecosystem, can be corroborated and tested by paleosynecologists. Despite severe methodological limitations of each paleoecological interpretation, the fossil record may under favorable taphonomic conditions enable an insight into the structure of ancient communities and ecosystems. The optimum strategy of research is to focuse at first on the recognition of empirical associations of organisms and thereafter, to evaluate their relations to environmental parameters. When this is accomplished, one may attempt to analyse the ecological structure of communities. Such an analysis should involve descriptions of both the autecology of dominant community members, and the taxonomic, trophic, and spatial structure of community. At last, communities can be compared to their extinct and extant analogues.

COGNITIVE PERSPECTIVE

Until some ten years ago evolution of the biosphere was, generally, regarded as a global effect of speciation and extinction processes acting on particular populations in changing environments. Hence, the interest of evolutionary scientists was focused mostly on the population level of biotic organization. This strategy of research was entirely consistent not only with the paradigm of biology, but also with classic analytic methodology of science which had postulated the resolution of observed phenomena into atomic entities and partial processes.

In a last few years the system point of view has, however, become more and more frequent. From this standpoint, the evolution should be first of all regarded as a process governed by the higher-order ecological organization. Speciation and species extinction are to be always considered as taking place in a framework delimited by the structure of ecosystem. Therefore, it is necessary to study not only populations and their evolutionary development through geological time, but also to

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solve the decisive problems found in the organization and order uni-
fying them into communities; the problems resulting from dynamic in-
teractions among populations which make the responses of populations
different when studied in isolation or within the whole ecosystem. In
other words, it is necessary to study complex relationships between the
structure and evolutionary behavior of a community and those of its
constituent populations.

Because of their enormous complexity, all these problems can be
successfully solved only by building models of biological processes and
their subsequent empirical testing. Derivation of a model involves ab-
straction of the accumulated informations into a form that can be more
easily understood. However, the simple collection of facts in the expec-
tation that some general relationships may become evident, does usual-
ly not allow to reasonably build up any model. In order to obtain an
adequate set of data, one must already possess some vague ideas or
preconceptions, some working hypotheses delimiting and organizing the
scope of the study, which are thereafter either verified, falsified, or
demonstrated to be incorrectly formulated. Moreover, one can perceive
and interpret facts only within the mental or psychological framework
of a paradigm (that is of a very general theory or even a world-view)
because it was clearly shown by all rationalistic critics of empiricism
that there are nopurely descriptive scientific terms (cf. Kuhn 1962).
Hence, even a° careful analysis of all informations available from pre-
viously collected data often appears insufficient to resolve either new
scientific problems, or old problems seen from a new perspective. Then,
new data are required.

Accumulation of data needed to build up evolutionary models rela-
ting the process of speciation and extinction to the ecological structure
within which it does take place, as well as to their empirical testing,
appears to be possible primarily by means of studies on the fossil re-
cord. This is why the analysis of structure and evolution of ancient
communities or ecosystems has become one of the most important fields
of paleontological work (cf. Shotwell 1958; Olson 1966; Bretsky 1969b;
Valentine 1973; Rollins & Donahue 1975; Walker & Allberstadt 1975;
Scott 1976). Studies on marine benthic communities appear especially
promising.

On the other hand, studies on extinct communities offer great po-
tential for fuller understanding of fossil species relationships with other
species, substrates, and physical factors not directly evident from the
sedimentological characteristics of deposits. They may also facilitate
the recognition of fine paleobiogeographical patterns and abiotic eco-
logical factors controlling these patterns. Thus, they may significantly
elucidate paleoclimatology, paleogeography, and facies development of

study areas (cf. Ziegler & al. 1968; Anderson 1971; Rhoads & al. 1972; Bowen & al. 1974; Thayer 1974; Hurst 1975; McGhee 1976).

Levins (1966) briefly discussed the strategy of model building in natural sciences and demonstrated that there is always a cost involved in model building since some variables, those regarded as unimportant, are discarded in order to better express important ones. This cost is either in degree of generality, degree of realism, or degree of precision. As shown by Levins (1966), only two of these three basic properties of a model can be satisfactorily considered. Schopf (1972) noted that up to date paleontological observations are generally concerned with precision and realism and hence, lack generality; while mathematical models postulated by the modern biological sciences possess generality and precision but lack realism. The extent to which a model can be relied upon, that is the extent to which a reasonable compromise between these divergent model properties is attained, is in part a function of the rigour with which it has been tested and corroborated.

METHODOLOGICAL PERSPECTIVE

When dealing with ancient populations, communities, or ecosystems, one should always keep in mind severe methodological limitations of each paleoecological interpretation. Two major lines of argument can be developed here. Firstly, paleoecological interpretations depend mostly on the application of a knowledge of living organisms to empirical patterns shown by fossils; while the probability of organisms and ecological structures undergoing differential adaptive trends at varying rates throughout geological time, and under the influence of changing composition of the lithosphere, hydrosphere, and atmosphere, tends to negate the reliability of such interpretations. Secondly, because of information losses resulting from different taphonomic processes, paleoecological data represent but a small and biased sample of the original community.

As pointed out by Lawrence (1968), one may distinguish three levels of validity of paleoecological inference, related to the significance of uniformitarian interpretations. In order of increasing validity these are: (i) reconstructions based solely or primarily upon the transfer of Recent data to ancient settings, (ii) observations on ancient strata supplemented by evidence from the Recent, and (iii) reconstructions made entirely from direct observations on ancient strata. In a later paper, Lawrence (1971) claimed that because of these differences in inference validity, paleoecological interests are to be focused mostly on either coaction (organisms acting upon organisms) or reaction (organisms acting upon physical environment), rather than on action relationships

(physical environment acting upon organisms). This claim appears reasonable although, on the other hand, the misleading role of uniformitarianism in paleoecology can be significantly diminished by considering adaptive morphology of both extant and extinct organisms. One may also suggest that when morphological similarity is observed along with similarity of occurrences (abundance, associated fauna, physical characteristics of environment) of fossil and Recent relatives, the extrapolation of informations on the biology of extant species to the fossil record attains a considerable degree of certainty.

Information losses and bias are mainly caused by either non-preservation of any traces of bodies or life activities of extinct organisms, or post-mortem transportation, sorting, and mixing of organic remains. Several studies on modern benthic communities demonstrated that the proportion of hard-shelled organisms which are potentially preservable may vary in a very wide range (cf. Johnson 1964; Craig & Jones 1966; Stanton 1976; Stanton & Dodd 1976). Therefore, all interpretations from the structure of a fossil assemblage must be made with caution. Nevertheless, one may recall many successfully accomplished studies on different geological formations ranging in age since Ordovician through Pleistocene to show that there are many paleoecological situations enabling such interpretations (cf. Bretsky 1969a; Walker 1972a; Watkins 1974a, b; Scott 1974; Wright 1974; Lespérance & Sheehan 1975; Stump 1975; Lenz 1976; Toomey 1976; Fürsich 1977). Furthermore, Lasker (1976) presented a method for a crude estimation of preservation bias.

As shown by extensive studies on modern marine environments, the significance of post-mortem transportation of skeletal remains has often been exaggerated. This process does, indeed, strongly affect communities living in intertidal or other high-energy environments. Nevertheless, as judged from the analyses of the spatial distribution of dead and alive specimens of subtidal benthic species, remains of shallow-water organisms are but rarely transported out of the gross environment in which they lived. Thus, the assumption that distribution patterns of fossil and original subtidal communities approximately coincide may be valid (cf. Johnson 1965; Cadée 1968; Warme 1969, 1971; Peterson 1976; Stanton 1976). More bias is probably introduced by the migration of either clusters of vagile benthic organisms, or patchy microhabitats, causing the origination of so-called time-averaged assemblages, that is assemblages resulting from a gradual accumulation of remains of biologically different communities (Walker & Bambach 1971).

In the fossil record some bias can also be introduced into a population or community structure by selective destruction of potentially preservable organic remains. This may be due to the life activities of certain scavengers or predators. However, selective breakage of shells by wave or current action or by compaction pressure, and selec-

tive solution of skeletal remains appear to be much more important factors in altering community composition and obscuring true ecological structure. Nevertheless, in subtidal environments the pre-burial selective destruction of potentially preservable organic remains is usually negligible, while the effects of post-burial processes can often be estimated (cf. Boyd & Newell 1972; Hallam 1972).

Thus, when carefully collected and interpreted with caution, all methodological limitations of paleoecological inference kept in mind, paleontological data may under favorable taphonomic conditions enable an insight into the structure of ancient communities and ecosystems. In fact, there exist several biotic and abiotic criteria by means of which one can assess the degree of post-mortem alteration of community composition and structure. These are: faunal composition, diversity, and density, fossils orientation, dispersion, disassociation, fragmentation, and surface conditions, size-frequency distributions of populations, sediment structure and texture (Johnson 1960; Fagerstrom 1964; Scott 1970; Lasker 1976). In general, seldom is it possible to evaluate all the criteria for every species in a fossil assemblage. Nevertheless, the final interpretation should always depend upon the evidence from as many criteria as can be reasonably applied.

When a minimum of post-mortem alteration can be evidenced, one may attempt to infer about the original community of living organisms. Such paleoecological situations permit a corroboration and test of evolutionary-ecological models, such as those of Sanders (1968, 1969), Bretsky & Lorenz (1970), Eldredge & Gould (1972), Valentine (1972), or Boucot (1975).

COMMUNITY CONCEPT

When an ecological study is intended to analyse the structure and behavior of a community, the community concept appears obviously as one of the key problems. As the matter of fact, the definition and notion of ecological community significantly differ among biologists. Some definitions take into account the habitat where a community occurs, while others are more or less independent of the physical environment. These concepts are discussed and clearly outlined by Newell & al. (1959) who recognized three major categories of ecological communities: (i) the organism community, defined strictly on a taxonomic basis as a recurrent group of species which are also numerically dominant; (ii) the habitat community, composed of natural association of populations occurring in a specified environment, and defined on the basis of a consistent linking of certain species with a physical environment or parameter; and (iii) the biocoenose, a community of organisms intimately related to one another and somewhat interdependent, that is a group of

populations that are actually associated in space and time and connected by a web of trophic interactions by which energy and nutrients flow through the ecosystem. Thus, both organism and habitat communities represent purely statistical constructions which ignore organism interrelationships, whereas the term biocoenose is to be applied when the ecological structure of a community is considered.

It is a major point of disagreement among marine biologists whether shallow-water benthic species are mutually interdependent and occupy non-overlapping niches in an equilibrium community, or whether they occur together because of similar responses to a given environment, being distributed each according to its own unique requirements. Johnson (1964) claimed that marine benthic species are largely independent of each other but directly dependent upon the physical-chemical environment (cf. also Jones 1950, Thorson 1957; Speden 1966). In other words, shallow-water benthic communities are to be considered as opportunistic rather than equilibrium communities, as physically rather than biologically controlled ecological units. If so, the term biocoenose would even not be applicable to these communities.

Nevertheless, it has recently been demonstrated that shallow-water benthic communities may show a highly complex and integrated structure which appears to be stable through ecological as well as geological time (Levinton & Bambach 1975; Peterson 1975; Stump 1975; Hoffman & Szulbzda 1976; Hoffman 1977). These results tend to support the approach of Parker (1975) who concluded that although microenvironments delimited by complex warter-circulation patterns and varying and diversified physical-chemical factors are characterized by small discrete patterns of species distributions, biotic interactions are extremely important toward maintaining the organization of these communities. Benthic populations do, indeed, shift their centers of abundance from one place to another. Moreover, they do dramatically increase or decrease in size in response to fluctuations in physical parameters. Nevertheless, given a particular habitat community, a web of biotic interrelations develops, imposing a fairly rigid framework on adaptive responses of the constituent populations. Therefore, benthic communities can be justifiably considered as actual associations of populations, controlled by continuously interplaying extrinsic and intrinsic factors. In fact, this concept appears also consistent with the holistic-methodologic approach suggested recently by Kauffman & Scott (1976).

RESEARCH STRATEGY

As noted by Speden (1966), in paleoecological studies the recognition of communities by distinctive associations of organisms is more subtle than by a physical parameter since slight environmental changes are

more quickly reflected in organisms than in the associated deposits. Therefore, the strategy of research should be to focuse at first on the recognition of organism communities and thereafter, to evaluate their relations to physical parameters, which permits the recognition of habitat communities. Only when this is accomplished, one may attempt to analyse the ecological structure of communities, that is to recognize the biocoenoses. This appears to be the only strategy enabling the recognition and subsequent analysis of homogeneous classes of paleoecological phenomena.

Then, the sampling problem appears as a crucial point in paleosynecological research. An ecological community can be characterized by a group of diagnostic species which are common in samples from within the community. Nevertheless, owing to a clearly polythetic (sensu Sokal & Sneath 1963) nature of benthic communities, none of these species is present in every sample, and none of these samples contains all diagnostic species (Valentine 1973). Therefore, the ability to recognize benthic communities is largely determined by the number and size of samples available. As shown by Stanton & Evans (1972), the sample size necessary to define or recognize a community is also strongly influenced by structural characteristics of the community. In general, it is inversely proportional to the homogeneity, dominance, and fidelity of the community. Furthermore, a large number of small independent samples offer much more reliability than a few large ones do, as it permits to diminish the bias introduced into the data by patchiness of distributional patterns of benthic species. On the other hand, when highly complex and taxonomically diverse communities are to be analysed, their ecological structures cannot be adequately studied by means of very small samples. The results of the recent study of Miocene macrobenthic communities of Poland (Hoffman & Szubzda 1976; Hoffman 1977) may suggest that samples consisting of less than some hundreds of specimens can hardly be used to reconstruct the structure of complex benthic communities.

When an adequate sample set is available, empirical distribution patterns of organisms can be analysed. These patterns are usually recognized by means of numerical analyses. Such an objective treatment permits to any number of investigators to obtain identical conclusions substantiated by identical numerical image of actual associations of organisms and their spatial distributions. Several more or less sophisticated numerical methods can be and actually were successfully applied to such ecological or paleoecological studies. Presence-absence data on all species occurring in a given set of ecological samples can be directly analysed by means of chi-square test or recurrent group analysis (Johnson 1962; Valentine & Mallory 1965; MacDonald 1975). Such data can also be transformed into any binary coefficient of association or other

similarity estimate, and subjected to any clustering technique (Kaesler 1966; Scott 1970; Warme 1971; Stanton & Evans 1971, 1972; Dodd & Stanton 1975; MacDonald 1975; Kojumdgieva 1976a, b, c). Relative-abundance data can be studied by means of ordination analysis (Park 1968; Gevirtz & al. 1971) or factor analysis (Howarth & Murray 1969; Guille & Ponge 1975; Parker 1975; McGhee 1976; Hoffman 1977).

However, all these methods are not equivalent. In fact, analyses of presence-absence data may overestimate the importance of rare species, whereas analyses of relative-abundance data may significantly underestimate them or even ignore at all. Field (1969) and Day & al. (1971) discussed the problem whether more meaningful results are to be obtained from an analysis of rare or common species. It has often been argued that rare species are more selective of environmental conditions and hence, better indicators of homogeneous habitats and organism associations than are common species tolerant of a fairly wide range of conditions. The counter argument is that while this may be true, the rare species are so subject to sampling errors that their distribution records do not give results as meaningful as do the records of common species. On the other hand, it was clearly shown by Parker (1975) that benthic communities differ not only in their taxonomic composition but also in density of their constituent populations, the latter characteristic being unreflected by the presence-absence data. Similarly, essential differences in structure among the Miocene benthic communities of Poland would be undetected by a presence-absence analysis since their overall taxonomic compositions were almost identical (Hoffman 1977; cf. also Kojumdgieva 1976a, b). In fact, this is not unexpected when benthic communities are regarded as intergrading communities of Johnson (1972). Therefore, it seems that the best and most reliable results are to be obtained from multivariate analyses of relative-abundance data. More specifically, the factor analysis of correspondences (Benzecri 1973; David & al. 1974) appears to be especially useful since it allows the use of continuously changing variables together with discontinuous and arbitrarily coded ones.

When empirical distribution patterns are recognized and the organism communities distinguished, the environmental parameters controlling animal distribution are to be analysed. Hence, the deposit associated with the samples should be studied very carefully. Unfortunately, there are many ecospace parameters unreflected at all in sedimentological characteristics of the deposit. Their recognition can be significantly facilitated by the use of R-mode multivariate analysis, such as factor or cluster analysis. R-mode factor or cluster axes themselves are to be regarded as purely abstract, mathematical constructs which permit relatively accurate location of a given large set of variables in a low--rank geometric space, and are usually assumed to be perpendicular

to, that is independent of each other. Nevertheless, these axes can also be thought of as the approximations of somewhat interdependent environmental characteristics or ecospace parameters. In fact, such an approach enables an insight into the nature and hidden structure of a continuous interplay among environmental processes which do actually control the observed diversity of ecological phenomena but cannot be directly observed or measured (cf. Imbrie 1964; Melguen 1973; Park 1974; Parker 1975; McGhee 1976; Hoffman 1977).

Thereafter, ecological structure of the communities distinguished can be studied. Ecological structure of a community is here meant as the whole of trophic and other biological interrelationships among all community members, and of their autecological relations to the abiotic environment. Hence, a basic characteristics of an ecological structure should always include several autecological analyses as well as more or less detailed analyses of taxonomic, trophic, and spatial structures of the community.

Taxonomic diversity is commonly assumed to be among the most important features of community structure. It is assumed to reflect the modal niche width and hence, the level of species interactions. It has been regarded as related to the seral stage in ecological succession, community stability, level of predation and competition, resource supply, habitat heterogeneity, climatic conditions, environmental stress or predictability (cf. Fischer 1960; MacArthur 1965; Pianka 1966; Spight 1967; Margalef 1968; Sanders 1968; Johnson 1970; Valentine 1971). On the other hand, validity and usefulness of diversity indices as measures of biotic complexity and degree of species interactions may be questioned because of biological as well as purely mathematical reasons (Goodman 1975; Moldenke 1975; Peet 1975). Nevertheless, even although the crucial importance of taxonomic diversity in ecological studies, that is its necessary relationship to environmental predictability or such essential community characteristics as successional maturity or stability, is not proved it should be extensively studied. As the matter of fact, several works on diversity gradients in portions of both extinct and extant communities (no matter whether these portions had been defined on the basis of purely taxonomic, ecologic, or preservability classifications) have demonstrated that this approach permits the recognition of important controls over organism communities (cf. Beerbower & Jordan 1969; Schopf 1970; Kafescioglu 1971; Stehli & Wells 1971; Gibson & Buzas 1973; Scott 1975).

When analysing the trophic structure of a benthic community, feeding types of the benthic taxa can be categorized accordingly to the recent discussion and classification by Walker & Bambach (1974). One should, obviously, keep in mind that many species cannot be ultimately ascribed to one feeding category or another because of their distinct

behavioral switch mechanisms (cf. Brafield & Newell 1961; Stasek 1965; Pohlo 1969). These difficulties in assigning consumer species to definite trophic categories and levels prompted Darnell (1961) to suggest that the term trophic spectrum is the most appropriate one. Nevertheless, one may claim that for the purposes of paleosynecological research even such a simplified classification may be adequate.

Competition for available space is usually most intense in hard-bottom communities (for the examples see Lewis 1964; Goldring & Kaźmierczak 1974; Palmer & Fürsich 1974). However, in soft-bottom communities a space-related competition may also considerably influence the ecological structure (Levinton & Bambach 1975; Stump 1975; Hoffman 1977). Therefore, spatial relations among the organisms at and just below the sediment-water interface should also be analysed in some detail.

At last, ecological structures of the communities studied can be compared to their ancient and modern counterparts. However, when highly complex biotic interactions are involved in community structure, the common practice of parallelizations based solely on dispersion of the total biovolume among different trophic levels or even less widely defined ecological groups (Bretsky 1969b; Walker & Laporte 1970; Walker 1972b) may be inadequate. In a strict sense, every change in either abiotic environment or constituent populations does change the structure since it always requires adaptive responses of more or less numerous populations. Nevertheless, almost exactly analogous niche complexes can be shared by ecosystems separated in both time and space (Wright 1974; Levinton & Bambach 1975; Watkins & Boucot 1975; Mares 1976; West 1976; Hoffman 1977); ecological niche is here considered as the totality of responses of an organism to all extrinsic stimuli. Therefore, in order to recognize two benthic communities different in their taxonomic composition as actually analogous in their structure, one must be able to recognize whether the criterion of a homeomorphy of the webs of biological interactions is violated or not. Then, besides vague dispersion of the total biovolume among gross ecological groups, the trophic webs and the levels of intragroup competition (or mechanisms buffering it) are to be also taken into account.

Thus, the optimum research strategy in paleosynecology of marine benthos can be briefly summarized as follows:
1. Choice of research area. Significance of taphonomic bias is to be carefully studied.
2. Adequate sampling. Large set of fairly large independent samples is needed, covering the whole ecological variability of research area.
3. Sample classification. Q-mode multivariate analysis of relative-abundance data is to be applied, in order to recognize homogeneous sample classes.

4. Environmental interpretation. R-mode multivariate analysis and independent sedimentological or paleontological evidence (when available) may allow to recognize the environmental control on benthic communities.

5. Structural analysis. Community structures are to be studied in detail, that is with trophic web, taxonomic diversity, and spatial relations taken into account.

6. Search for structural counterparts. Finally, the recognized biocoenoses can be compared to their ancient and modern counterparts, which may permit further evaluation of evolutionary-ecological models.

In fact, this strategy has recently been applied to synecological study of the abundant and well preserved macrobenthos of the Badenian (Miocene) Korytnica Clays, Poland (Hoffman 1977). The analysis permitted to further refine the knowledge of environmental conditions in the Korytnica basin. Moreover, the results were used to test but failed to corroborate the time-stability hypothesis of Sanders (1969) and some of its derivatives.

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STRESZCZENIE

W ostatnich latach ewolucję biologiczną traktuje się coraz częściej
jako proces w znacznym stopniu uzależniony od organizacji ekologicz-
nej biosfery. Jeśli przyjąć ten punkt widzenia, to badacze ewolucji nie
mogą się ograniczać jedynie do studiów nad poszczególnymi gatunkami,
ale muszą się również zagłębiać w problematykę ekologicznych związ-
ków pomiędzy populacjami i ich wpływu na ewolucję gatunków. To
właśnie dlatego analiza struktury i ewolucji biocenoz kopalnych na-
brała ostatnio takiego znaczenia. Szczególnie popularne są badania nad
płytkowodnym bentosem morskim. Dzieje się tak dlatego, że analizy
tego typu mogą się również — przy okazji — poważnie przyczynić do
lepszego poznania warunków klimatycznych, paleogeografii i rozwoju
facjalnego badanych obszarów.

Oczywiście, każde wnioskowanie paleoekologiczne obwarowane jest
poważnymi ograniczeniami metodologicznymi. Po pierwsze bowiem —
wszelkie interpretacje oparte ściśle na rozumowaniu aktualistycznym za-
wierają dość duży margines błędu. Po drugie zaś — rozmaite procesy
tafonomiczne powodują, że paleoekolog dysponuje jedynie niewielką,
a często niereprezentatywną próbką pierwotnej biocenozy. Niemniej
jednak gruntowna analiza litologii oraz składu i stanu zachowania sa-

mych skamieniałości pozwala przynajmniej oszacować znaczenie tych procesów. Gdy na podstawie wielu niezależnych od siebie kryteriów uda się stwierdzić, że owe procesy tafonomiczne były nieistotne, uprawnione jest wnioskowanie o charakterze pierwotnej biocenozy.

Zasadniczym, a bynajmniej nie trywialnym problemem jest, rzecz jasna, kwestia definicji biocenozy. Pojęcie to jest bowiem wśród ekologów (a zwłaszcza — ekologów morza) rozmaicie rozumiane. Najnowsze badania zdają się wskazywać, że płytkowodne biocenozy bentoniczne miewają skomplikowaną i zintegrowaną strukturę ekologiczną stabilną w czasie ekologicznym i trwałą w czasie geologicznym. Potwierdza to zasadność definiowania biocenoz tego typu jako grupy współwystępujących populacji kontrolowanych nie tylko przez czynniki fizykochemiczne, ale i przez wzajemne oddziaływania biologiczne.

Drugi zasadniczy problem to kwestia właściwego opróbowania badanego obszaru. Biocenozę można scharakteryzować przy pomocy grupy diagnostycznych gatunków. Trzeba jednak pamiętać, że z reguły żadna próbka nie zawiera wszystkich diagnostycznych gatunków, a żaden gatunek nie występuje we wszystkich próbkach. Co więcej, rozkład przestrzenny zwierząt bentonicznych na dnie morza bynajmniej nie jest jednorodny. Dlatego duża liczba niewielkich próbek zapewnia danym większą wiarygodność niż kilka dużych próbek. Z drugiej strony, wydaje się, że struktury skomplikowanych biocenoz bentonicznych nie można adekwatnie opisać na podstawie próbek mniejszych od kilkuset okazów.

Po pobraniu odpowiedniego zbioru próbek trzeba zbadać rozkład przestrzenny poszczególnych gatunków bentonicznych na rozważanym obszarze. Idzie o to, by cały zbiór próbek podzielić na homogeniczne grupy reprezentujące pierwotne biocenozy. Zazwyczaj dokonuje się tego przy pomocy analizy numerycznej. Metody numeryczne mają bowiem walor obiektywności rozumianej w tym sensie, że na podstawie tych samych danych każdy badacz dojdzie do tych samych wniosków. W ekologii i paleoekologii stosuje się rozmaite metody analizy numerycznej. Wydaje się jednak, że najlepsze rezultaty daje analiza czynnikowa typu Q danych o względnej częstości występowania poszczególnych gatunków bentonicznych w próbkach. Szczególnie korzystne są wszelkie algorytmy pozwalające wprowadzać do macierzy danych zarówno zmienne ciągłe, jak i nieciągłe.

Kiedy się już wyodrębni grupy próbek reprezentujące oddzielne biocenozy, trzeba zbadać, jakie fizykochemiczne czynniki środowiska decydują o takim właśnie rozkładzie przestrzennym rozważanych gatunków. Należy w tym celu przeanalizować wszelkie dostępne cechy litologiczne i paleontologiczne. Niestety, wiele istotnych parametrów środowiska nie pozostawia po sobie żadnych bezpośrednich śladów w osadzie czy skamieniałościach. Do ich wykrycia można zastosować analizę czynni-

kową typu R badanej macierzy danych (względna częstość występowania gatunków bentonicznych w poszczególnych próbkach). W zasadzie osie czynnikowe typu R to czysto abstrakcyjne konstrukcje matematyczne pozwalające zredukować rząd hiperprzestrzeni bez żadnej istotnej zmiany zależności pomiędzy badanymi próbkami. Na ogół zakłada się, że osie te są do siebie prostopadłe, to znaczy — wzajemnie niezależne liniowo. Niemniej, można je również potraktować jako przybliżenie współzależnych w pewnej mierze parametrów ekologicznych. Pozwala to wejrzeć w ukrytą strukturę procesów ekologicznych kontrolujących obserwowane zjawiska.

Po zinterpretowaniu parametrów środowiska można już przystąpić do analizy struktury ekologicznej wyodrębnionych biocenoz. Przez strukturę biocenozy rozumie się tutaj sieć zależności biologicznych pomiędzy poszczególnymi populacjami oraz związki tych populacji z biotopem. Opis struktury ekologicznej powinien zatem zawierać analizy autekologiczne poszczególnych populacji oraz mniej lub bardziej precyzyjny opis struktury taksonomicznej, troficznej i przestrzennej samej biocenozy.

Wreszcie — strukturę wyodrębnionych biocenoz porównać można z ich kopalnymi i współczesnymi odpowiednikami. Trzeba przy tym pamiętać, że przy analizie skomplikowanych struktur ekologicznych nie wolno się ograniczać do porównywania rozkładu bioobjętości pomiędzy poszczególne poziomy czy grupy troficzne. Po to, żeby dwie biocenozy odmienne pod względem składu taksonomicznego uznać za analogiczne pod względem struktury ekologicznej, trzeba sprawdzić, czy ich struktury spełniają warunek homomorfizmu. W tym celu trzeba zbadać ich sieci troficzne i rolę konkurencji wewnątrz grup ekologicznych.

Opisaną tutaj strategię badawczą zastosowano niedawno do analizy synekologicznej makrobentosu iłów korytnickich (miocen). Analiza ta pozwoliła uściślić i uzupełnić wiedzę o warunkach ekologicznych panujących w basenie korytnickim. Jej wyniki zdają się również podważać teorię ekologiczną postulującą istnienie korelacji pomiędzy złożonością struktury ekologicznej a jednostajnością warunków fizykochemicznych w biotopie.