acta
geologica
polonica

Vol. 28, No. 3 Warszawa 1978

ANTONI HOFFMAN, ANDRZEJ PISERA & WIESŁAW STUDENCKI

Reconstruction of a Miocene kelp-associated macrobenthic ecosystem

ABSTRACT: Original ecological structure of a Miocene macrobenthic, mostly mollusk, assemblage of Łychów, southwestern part of the Lublin Upland, Central Poland, is restored. The paleoecosystem is recognized for a kelp bed, with browsing and epifaunal suspension feeding animals forming two dominant subsystems. Loose shelly substrate is recognized for the keystone abiotic factor determining the ecological structure. Paleoecosystem reconstruction is in terms of system analysis which are proposed for a standard descriptive language for community paleoecology.

INTRODUCTION

The aim of this community-oriented paleoecological study is to restore the original ecological structure of a macrobenthic, mostly mollusk assemblage occurring at Łychów, southwestern part of the Lublin Upland, Central Poland; in fact, the Miocene sediments exposed at that locality are well known to comprise an abundant, excellently preserved, and highly diverse fauna (Krach 1962, Bielecka 1967, Jakubowski 1972, Radwański 1977). To this end, however, to find out an adequate descriptive language appears as a necessary prerequisite, since after the initial impetus a dozen years ago, further developments in the field of community paleoecology have become strongly hampered by the apparent cloudiness of both the concepts and terms. It is here claimed that the system-analytic approach derived from the modern economics and organization science may appear relevant to the problem, as it permits a simple graphical representation of ecological systems to be compared through time; while no precise quantitative data are required.

Acknowledgments. The authors wish to express their most sincere thanks to Docent W. Bałuk, Warsaw University, for his help in identification of the fossils.

GEOLOGICAL SETTING

The investigated locality Łychów is at the northern margin of the Fore-Carpathian Depression (Fig. 1). In that area, the Miocene deposits are relatively thin (20 to 40 m) and lithologically variable. They include sands, clays, marls, detrital limestones, and algal-vermetid reefal limestones; all the sediment types are always very fossiliferous. The spatial relationships among the Miocene lithofacies are strongly obscured by the Quaternary cover and two faults systems (regional NW-SE, and local NE-SW) making almost impossible any precise correlations. Therefore, the exposure referred generally to as Łychów (southern slope of the valley of Karasiówka river, near the center of the village) cannot be treated within any clear facies framework.

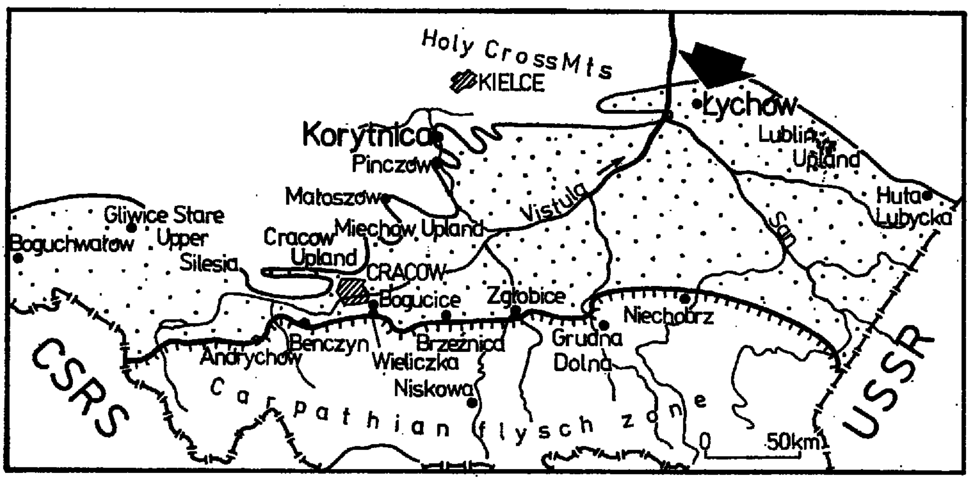

Fig. 1. Paleogeographical setting of the Łychów exposure (*arrowed*) within the range of the Miocene (Badenian) deposits (*stippled*) of the Fore-Carpathian Depression in southern Poland; indicated are well-known fossiliferous localities (*from* Radwański 1977, p. 742 — Text-fig. 169)

In that exposure, the Miocene fossiliferous glauconitic sands, marly clays, and coquinites overlie directly the Cretaceous limestones; however, the contact zone is inaccessible. The Miocene thickness does probably not exceed 4 m. A detailed vertical section of the considered strata was given by Bielecka (1967); unfortunately, the figure seems to be unreliable, as the lithologies found by the present authors are incompatible with it. In fact, a considerable horizontal lithological variability can also be expected.

Judging from their extremely rich fossil assemblage, the investigated sediments are to be assigned to the Lower Badenian. However, their precise stratigraphic position remains unclear. One may but claim that the considered strata are equivalent to (or maybe partly younger than) the algal-vermetid reefal limestones cropping out in the neighborhood (Pisera 1978). In fact, marly clays resembling closely in both the lithology and fauna those exposed at Łychów do overlie the reefal limestones at Węglin (2 km to the west). In the south, the fossiliferous sands and clays and the reefal limestones are replaced with the detrital limestones and the oyster- and scallop-bearing marls.

The overlying Upper Badenian deposits are detrital in nature and often cross-bedded; their fossil assemblages are rather poor and indicative of non-normal marine conditions.

FOSSIL ASSEMBLAGE

In order to recognize the fossil assemblage characteristic of the Miocene of Łychów composed mostly of mollusks (Table 1), 8 independent bulk samples (each of a few kilograms in weight) were taken from various lithologies and their taxonomic composition carefully analysed; in addition, surface collecting was also done. Totally, some thousand specimens were investigated (the collection is housed at the Institute of Geology, University of Warsaw). Precise taxonomic work was beyond the scope of the present study and hence, the names associated traditionally with the fossil species are usually retained. The samples resemble each other in taxonomic constitution eventhough the proportions among the taxa may vary. In fact, it appears reasonable to claim that they represent a single, more or less homogeneous biological community persisting under the same ecological conditions over a fairly long time. Therefore, the averaged results were interpreted directly in ecological terms, assuming that they do reflect, at least in first approximation, the original community; this is, indeed, suggested by the uniform excellent preservation state of the fossils, the large variety of modal size values among the species, and the ecological coherence of the assemblage. In the present paper, all autecological characteristics of the fossils are based upon the informations on their extant relatives.

Table 1

List of mollusks making up the investigated assemblage from Łychów, as determined by the authors

GASTROPODS:

Acmaea sp
Alaba costelata anomala (Eichwald)
A. zboroviensis Friedberg
Alaba sp.
Alvania oceani (d'Orbigny)
A. tenuicostata Bałuk
A. montagui ampulla (Eichwald)
A. perregularis (Sacco)
Aspella anceps (Lamarck)
Bellardiella sp.
Bittium reticulatum (da Costa)
B. turritella (Eichwald)
Calliostoma puberum (Eichwald)
C. planatum Friedberg
C. celinae (Andrzejowski)
Cantharus exculptus (Dujardin)
C. beregovi Kojumdgieva
Cerithiopsis tuberculatus (Montagu)
Cerithium vulgatum europaeum Mayer
Cerithium sp.
Clanculus araonis tuberculatus (Eichwald)
Clanculus sp.
Columbella sp.
Cypraea sp.

Conus spp.
Diodora graeca (Linnaeus)
Emarginula sp.
Fossarus costatus (Brocchi)
Gibbula affinis affinis (Eichwald)
G. affinis pseudangulata Boettger
Haliotis sp.
Hydrobia sp.
Janiopsis sp.
Manzonia costata (Adams)
M. zetlandica (Montagu)
M. scalaris (Dubois)
Mitraria sp.
Mitrella hilberi (Cossmann)
Mitrella sp.
Murex spp.
Muricopsis sp.
Nassa serraticosta (Bronn)
Natica sp.
Odontostomia plicata (Montagu)
Patella neglecta oblita Michelotti
Peratotoma unica Boettger
Pyrgulina sp.
Ringicula sp.
Rissoina podolica Cossmann
R. decussata (Montagu)
R. vindobonensis Sacco
R. steinabrunnensis Sacco
Sandbergeria spirallissima (Dubois)
Setia trilineata (Philippi)
Thais hemastomoides (R. Hoernes & Auinger)
Tornatina truncatula (Bruguière)
Triphoris sp.
Turboella acuticostata Sacco
Turbonilla scala (Eichwald)
Turriculata recticostata (Bellardi)
T. ebenus (Lamarck)
T. partschi (Hoernes)
Vermetus spp.
Vermicularia sp.

BIVALVES:

Arca lactea Linnaeus
A. noae Linnaeus
Barbatia clathrata (Defrance)
B. barbata (Linnaeus)
Cardium holubicense Hilber
C. praeechinatum Hilber
Chama gryphoides Linnaeus
Chlamys multistriata Poli
Codakia decussata (da Costa)
Coralliophaga transilvanica (Hoernes)
Corbula gibba (Olivi)
Dosinia exoleta (Linnaeus)
Ervilia pusilla Philippi
Gastrana fragilis (Linnaeus)
Glycymeris pilosa deshayesi (Mayer)
Isognomon sp.
Lima lima Linnaeus
Lithophaga sp.
Loripes dentatus niveus (Eichwald)
Lutetia sp.
Modiolus hoernesi (Reuss)
Modiolaria biformis (Reuss)
Ostrea spp.
Plicatula ruperella Dujardin
Septifer oblitus (Michelotti)
Spondylus sp.
Timoclea sp.
Venerupis irus (Linnaeus)
Venus cincta Eichwald

The assemblage is predominated by diverse gastropods (*cf.* Table 1), mostly various herbivorous rissoids, cerithiids, and trochids. A cerithiid, *Bittium reticulatum* appears as the most common species; in fact, it ranks the first abundant species in all but one sample. The species *Rissoina podolica, Alaba* sp., *Alvania montagui ampulla, Calliostoma planatum, Gibbula affinis pseudangulata,* and *Clanculus araonis tuberculatus* are also among the most common taxa. On the other hand, a sessile epifaunal suspension feeder *Vermetus* sp. occurs abundantly in virtually all the samples, becoming predominant in a single sample; interestingly, the latter sample is also considerably enriched in coralline-algal fragments. Other gastropods represent mostly higher trophic levels and include a scavenger *Nassa serraticostata,* parasitic pyramidellids *Turbonilla scala, Odontostomia plicata, Pyrgulina* sp., and diverse predators as e.g. *Thais hemastomoides, Turricula recticostata, Cypraea* sp., and *Conus* spp.

The gastropods are accompanied by several bivalve species (*cf.* Table 1), with epibyssate arcids, mytilids, and pectinids as the most characteristic groups. The species *Septifer oblitus* does also occur fairly commonly (*cf.* Jakubowski 1972). In a single sample, an infaunal rapidly burrowing suspension feeder *Ervilia pusilla* occurs very abundantly; it is noteworthy that related species live today in shifting sands. In another sample, some amphineuran plates were recorded.

Aside of the mollusks, the assemblage includes also unidentified polychaetes, bryozoans, crabs, cirripedes *Verruca* sp., and brachiopods *Argyrotheca subcordata* (Boettger).

Taxonomic diversity of the assemblage was not quantified. Nevertheless, it can be certainly assessed as extremely high, comparable to the most diverse Miocene macrobenthic assemblages of Poland. Totally, more than one hundred mollusk, one brachiopod, and one cirripede species were recognized. Furthermore, the dominance is rather low, as a group of some five to seven species rank similarly in abundance, while a dozen or so other species do also occur commonly. As reflected by the between-sample variability, homogeneity of the assemblage was fairly high.

The fossil density is extremely high. Indeed, the inorganic sediment occurs but very subordinately to the shells themselves. One may even claim that its amounts were insufficient to make the substrate cohesive to any reasonable extent. With the lack of evidence for any considerable post-mortem transportation taken into account, this may indicate both an extremely rich organic life in the environment and a very low sedimentation rate.

SYSTEM-ANALYTIC APPROACH

Since the classic papers by Olson (1966), Valentine (1968), and Bretsky (1969) appeared, the evolution of communities and its relationship to the evolution of species have become one of the most pervasive topics in paleoecology. Nevertheless, any standard procedures or even terms for paleocommunity description are lacking and consequently, the data gathered and presented by different authors are often incompatible. Moreover, even the most detailed paleocommunity reconstructions do usually disregard species-biotope relationships, while it seems indispensable to consider a community structure in terms of the totality of ecological niches, that is the totality of biotic and abiotic ecospace dimensions limiting the community members. This is probably mainly due to the extreme complexity of structures to be dealt with. Then, the system-analytic approach appears relevant because it is intended (among other aims) to provide a descriptive language adequate to such enormously complex subjects as *e.g.* the economic structure of the world and its dynamics.

When considering an ecosystem in terms of the system analysis (*cf.* Forrester 1971), it can be adequately represented with the use of but two kinds of variables, namely levels and rates (or flows). The levels describe precisely the system state at any point in time; they are caused to change by the flows. They arise as accumulations of net differences between the flows that add to and subtract from subsystems. In every ecosystem, there are resource and population levels resulting from the influx and usage rates and the birth and death rates, respectively.

There are five basic resources in a shallow-water benthic ecosystem. These are: suspended organic matter, deposited organic matter, benthic plants, epispace, and inspace. They are, obviously, interrelated, as benthic plants contribute to deposited organic matter and the latter may be resuspended and again redeposited and so on; benthic plants are also dependent upon epispace for attachment but in turn, they contribute to the latter resource. The resource levels in an ecosystem depend upon the respective influx rates controlled by various environmental parameters. In turn, the resource levels make possible animal life in an environment. The population levels control, however, the resource-usage rates and by this way, influence the resource levels. There are the following basic ecological categories of animal populations in shallow-water benthic ecosystems: browsers, infaunal and epifaunal scavengers, infaunal and epifaunal deposits feeders, infaunal and epifaunal predators and parasites. Clearly, not all resources do actually control all the population categories. Hence, various subsystems arise in an ecosystem. The population levels depend upon their respective birth and death rates controlled not only by the population levels themselves and the resource levels but also by various environmental factors. Moreover, the population levels are also strongly dependent upon the predation rates since apart from a few keystone predators, virtually all animals appear as a prey, that is food resource, for one or more predator species. The structure of a shallow-water benthic ecosystem can thus be diagrammatically represented (Fig. 2) as composed of three successive stages, *viz.* the resources, low trophic-level consumer populations, and predator populations. Every two successive stages are interconnected by resource and information flows generating diverse feedback loops. Feedback loop is here meant as a closed path connecting an action to its effect and sending back the information on the effect to influence further action. At each stage, the levels are also controlled by system-independent environmental parameters.

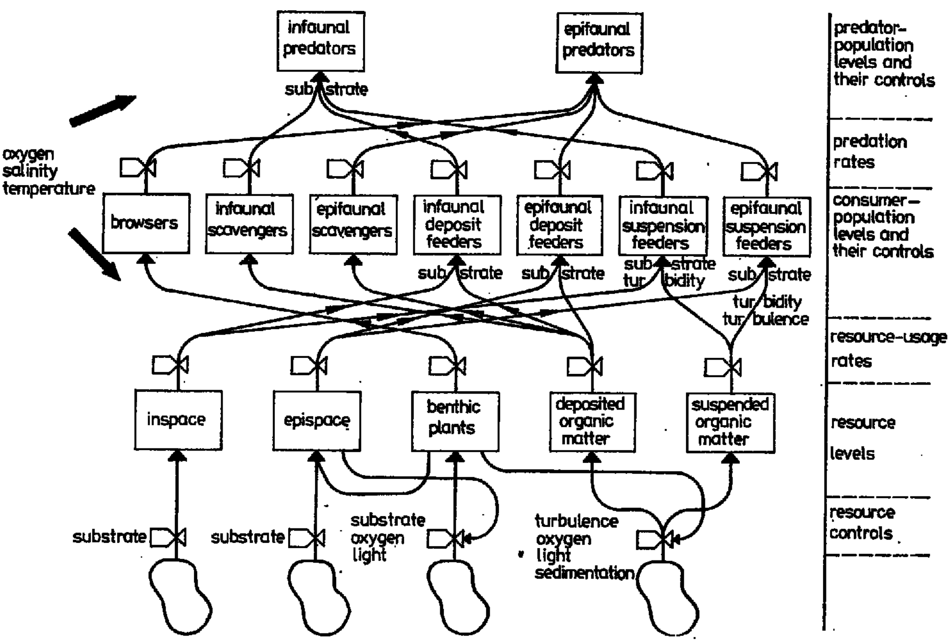

Fig. 2. Diagrammatic structure of a shallow-water benthic ecosystem

Limiting abiotic factors are given in bold letters; for details of the feedback loops controlling the resource-usage rates, population levels, and predation rates see Fig. 3

clouds system-independent states, *rectangles* levels, *arrows* rates (or flows), *faucets* rate controls

Consider a single low trophic-level consumer population and a resource it uses (Fig. 3). When the population grows, its birth rate increases and hence, the population does increase more and more. Positive feedback loops of this type induce growth in an ecosystem. The death rate does also increase with the population growth, hampering it. Negative feedback loops of this type tend to equilibrate an ecosystem. When the population grows, the resource-usage rate grows, too, and hence, the resource ratio (the amount of resource *per capita*) decreases causing a decrease in the birth rate and an increase in the death rate. Thus, negative feedback loops arise. All the rates involved in this interaction are also dependent upon various environmental parameters. An entirely analogous set of feedback loops arises between a predator and its prey population. When two populations of the same stage compete for a resource, they both contribute to the controls upon the resource-usage rate and hence, the resource ratio. By this way, additional negative feedback loops arise. To quantify all those feedback loops in real ecosystems is among the most important tasks of neoecologists. This is, obviously, impossible in the fossil record. In order to justify the qualitative approach, one may, however, recall the recently introduced method of loop analysis intended to deal with qualitative structural data and its resolving potential (Levins 1975).

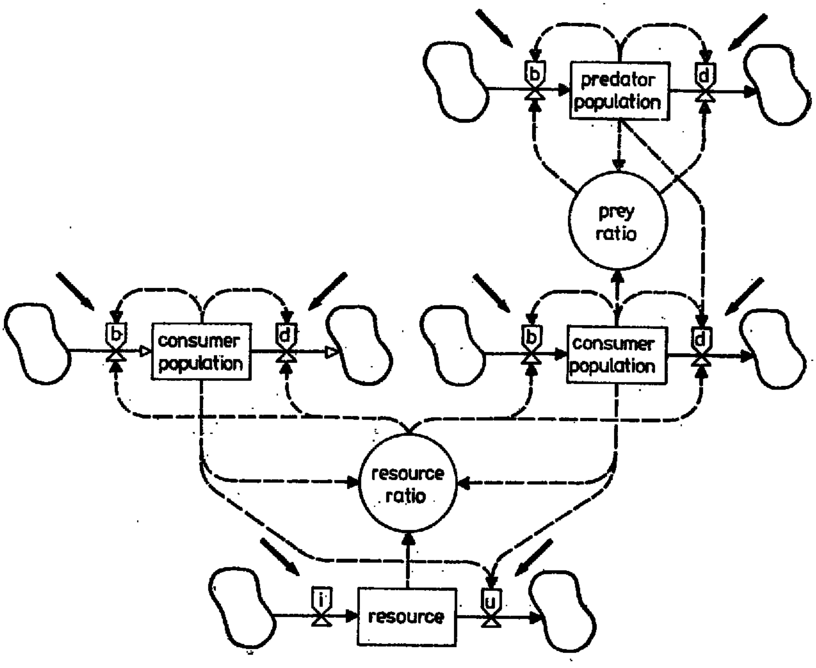

Fig. 3. Feedback loops controlling resource-usage rates, population levels, and predation rates in competitive and predator-prey interactions

clouds system-independent states, *rectangles* levels, *solid arrows* rates (or flows), *faucets* rate controls, *dashed arrows* information flows, *thick arrows* environmental influences, *circles* specified links in feedback loops

b birth rate, *d* death rate, *i* resource-influx rate, *u* resource-usage rate

With this complex nature of within-stage and between-stage feedback loops (Fig. 3) kept firmly in mind, the simplified diagram (Fig. 2) appears adequate to the purposes of community paleoecology. In general, the resources are not fully exploited in benthic ecosystems. Therefore, the resource levels depend mostly upon environmental parameters rather than upon the population levels. All the population levels are controlled by some common ecospace dimensions, namely the oxygen content, water salinity and temperature. Particular ecological categories depend also each upon some specific environmental factors such as the substrate nature or water turbidity.

The diagram is advantageous in that it can be expanded both laterally and vertically. In fact, one can easily add new predator stages to the system. On the other hand, the resources and ecological categories can be further subdivided. One may analyse separately *e.g.* the shallow and deep inspace, or the dissolved and detrital organic matter; the high-level suspension feeders can also be distinguished from the low-level ones, and the collecting deposit feeders from the swallowers. Furthermore, a single ecological category can always be split down into particular species to show their competitive interactions. Limiting abiotic factors can always be clearly stressed. The main disadvantage of the method is in that it disregards taxonomic diversity of communities. However, validity of diversity indices as measures of ecological complexity or modal niche size can be seriously cast into doubt (*cf.* Goodman 1975, Moldenke 1975).

PALEOECOSYSTEM RECONSTRUCTION

The paleoecosystem represented by the investigated Miocene macrobenthic assemblage fits well to the above presented system-analytic framework (Fig. 4). The community was clearly dominated by abundant and diverse browsers and epifaunal suspension feeders; all other low trophic-level consumer categories played but minor roles or even were absent at all. This is typical of shallow-water communities associated with large benthic plants supplying a lot of epispace for both microflora and fauna. However, the browsers do usually feed upon epiphytal microalgae and diatoms and hence, are not indicative of either seagrass or kelp beds; neither are specific the epibionts (*cf.* Sloane & *al.* 1961, Lewis 1964, Warmke & Almodovar 1964, Hagerman 1966, Duffus 1969, Brasier 1975, Parker 1975). Nevertheless, the kelp nature of Łychów paleoecosystem recognized the first by Radwański (1977) is indicated clearly although indirectly by the substrate nature[1]. In fact, seagrasses are unable to root themselves in such an incohesive substrate as it appears to have occurred at Łychów; while large algae could attach each to several larger shell fragments buried deep in the sediment and by this way, stabilize themselves. The investigated ecosystem would thus resemble that one recorded by Andrews (1945) in sand and gravel bottom areas of California Bay. The *Bittium*-dominated communities are also commonly adapted to fluctuating salinity conditions (Dr. B. K. Ghose, *pers. communication*). However, the extreme diversity of mollusk and other invertebrate life precludes such a possibility in the case of Łychów paleoecosystem.

---

[1] In other localities that yield similar, gastropod-dominated assemblages in the Fore-Carpathian Miocene, the kelp environment was previously postulated also by Friedberg (1928, p. 321).

Then, the loose shelly substrate appears as the keystone abiotic factor determining the entire ecological structure. Actually, it caused the lack of both inspace and primary epispace in the ecosystem; the former because animals are usually unable to burrow in such a sediment (*Ervilia* being apparently an exception), the latter because of the substrate mobility. Large amounts of epispace were, however, secondarily produced by the

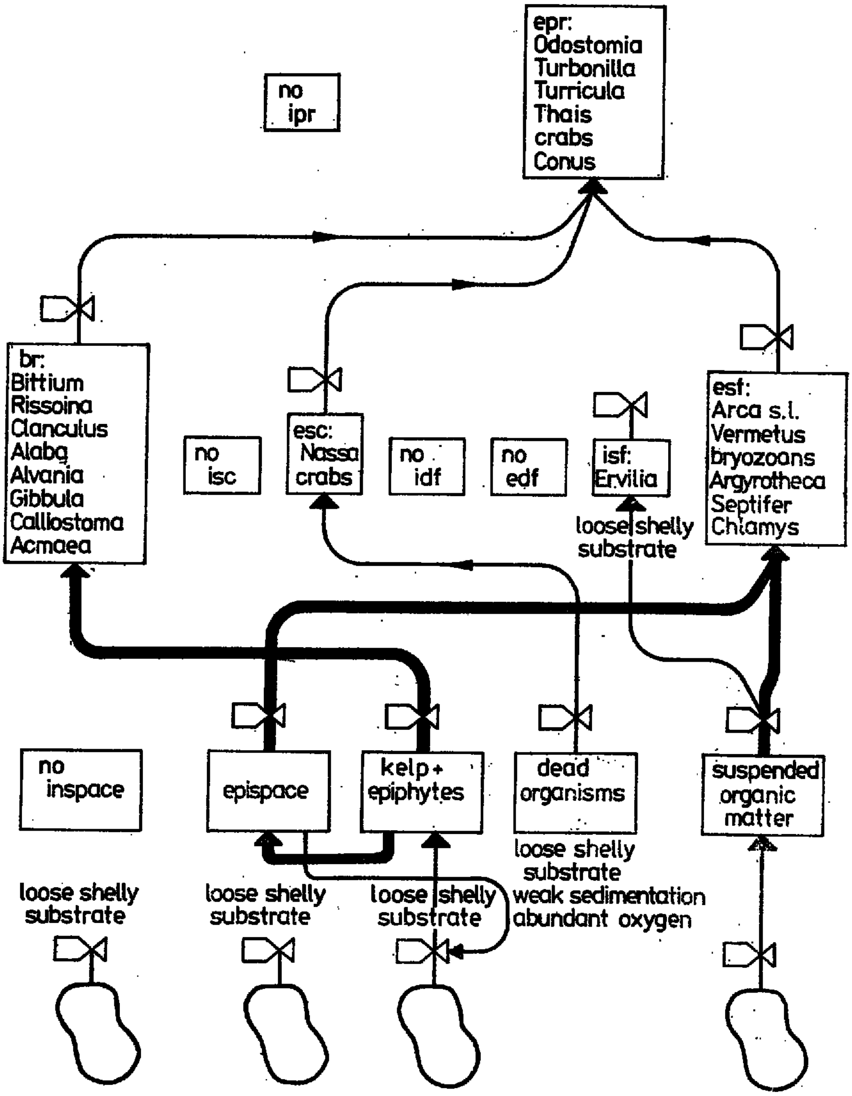

Fig. 4. Reconstruction of Łychów paleoecosystem

Width of the arrows indicates relative significance of the resource flows; for explanation of other graphical symbols see Fig. 2

br browsers, *isc* infaunal scavengers, *esc* epifaunal scavengers, *idf* infaunal deposit feeders, *edf* epifaunal deposit feeders, *isf* infaunal suspension feeders, *esf* epifaunal suspension feeders, *ipr* infaunal predators and parasites, *epr* epifaunal predators and parasites kelp. Along with the weak sedimentation and high oxygen content, the loose shelly substrate resulted also in very rapid decay of the organic matter. Therefore, no deposited organic matter was available in the ecosystem apart from newly dead organisms permitting the life of some scavengers. Both the main subsystems, that is the browsing and epifaunal suspension feeding ones, represented actually clusters of parallel largely independent chains; in fact, one can hardly imagine the considered animal populations to be large enough to have been resource-limited. Then, the ecosystem was probably rather simple ecologically even despite the apparent taxonomic diversity of the animal life.

The geological isolation of the exposure and the general eurytopy of both kelp itself and its associated macrofauna do not allow to draw any more detailed paleoenvironmental conclusions than the obvious inference of the shallow-water normal-marine conditions.

Wiejska 14 m. 8,
00-490 Warszawa, Poland
(A. Hoffman)

Institute of Geology
of the Warsaw University
Al. Żwirki i Wigury 93,
02-089 Warszawa, Poland
(A. Pisera)

Museum of the Earth
(Polish Academy of Sciences),
Al. Na Skarpie 20/26,
00-488 Warszawa, Poland
(W. Studencki)

REFERENCES

ANDREWS H. L. 1945. The kelp beds of the Monterey region. *Ecology*, **26** (1), 24—37 Brooklyn.

BIELECKA M. 1967. The Tertiary of the south-western part of the Lublin Upland. *Biul. IG*, **206**, 115—188. Warszawa.

BRASIER M. D. 1975. An outline history of seagrass communities. *Palaeontology*, **18** (4), 681—702. London.

BRETSKY P. W. 1969. Evolution of Paleozoic benthic marine invertebrate communities. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **6** (1), 45—59. Amsterdam.

DUFFUS J. H. 1969. Associations of marine Mollusca and benthic algae in the Canary Island of Lanzarote. *Proc. Malacol. Soc. London*, **38** (4), 343—349. London.

FORRESTER J. W. 1971. World Dynamics. *Wright-Allen Press;* Cambridge, Mass.

FRIEDBERG W. 1928. Études dur le miocène de la Pologne, Partie IV. *Kosmos, Ser. A*, **53** (2/3), 313—325. Lwów.

GOODMAN D. 1975. The theory of diversity-stability relationship in ecology. *Quart Rev. Biol.*, **50** (3), 237—266. Cambridge, Mass.

HAGERMAN L. 1966. The macro-microfauna associated with *Fucus serratus* L, with some ecological remarks. *Ophelia*, **3**, 1—43.

JAKUBOWSKI G. 1972. Ontogeny of some pelecypod shells from the Miocene of Poland. *Prace Muzeum Ziemi (Trans. Museum of the Earth)*, **20**, 45—117. Warszawa

KRACH W. 1962. Stratigraphy and fauna of the Miocene in the vicinity of Zaklików and Modliborzyce (Lublin Upland). *Prace IG*, **30** (3), 417—447. Warszawa.

LEVINS R. 1975. Evolution in communities near equilibrium. *In:* M. L. CODY & J. M. DIAMOND (*Eds*), Ecology and Evolution of Communities, 16—50. *Belknap Press;* Cambridge, Mass.

LEWIS J. R. 1964. The Ecology of Rocky Shores. *English Universities Press;* London.

MOLDENKE A. R. 1975. Niche specialization and niche diversity along a California transsect. *Oecologia*, **21** (2), 219—242. Berlin.

OLSON E. C. 1966. Community evolution and the origin of mammals. *Ecology*, **47** (2), 291—302. Brooklyn.

PARKER R. H. 1975. The Study of Benthic Communities. *Elsevier;* Amsterdam.

PISERA A. 1978. Miocene reef deposits of the Western Roztocze. *Przegl. Geol.*, No. 3, 159—163. Warszawa.

RADWAŃSKI A. 1977. Neogen. *In:* H. MAKOWSKI (*Ed.*), Geologia historyczna [Historical Geology (*in Polish*)], 731—770. *Wyd. Geol.;* Warszawa.

ŚLOANE J. F., BASSINDALE R., DAVENPORT E., EBLING F. J. & KITCHING J. A. 1961. The ecology of Lough Ine. *IX.* The fauna and flora associated with undergrowth forming algae in the rapids area. *J. Ecology*, **49** (3), 353—368. Cambridge.

VALENTINE J. W. 1968. The evolution of ecological units above the population level. *J. Paleontology*, **42**, (2), 253—267. Menasha.

WARMKE G. L. & ALMODOVAR L. R. 1964. Some associations of marine mollusks and algae in Puerto Rico. *Malacologia*, **1** (2), 163—177. Ann Arbor.

A. HOFFMAN, A. PISERA & W. STUDENCKI

REKONSTRUKCJA MIOCEŃSKIEJ BIOCENOZY MAKROBENTONICZNEJ Z ŁYCHOWA NA WYŻYNIE LUBELSKIEJ

(Streszczenie)

Przedmiotem pracy jest rekonstrukcja mioceńskiej biocenozy makrobentonicznej reprezentowanej przez zespół skamieniałości z Łychowa na Wyżynie Lubelskiej (*patrz* fig. 1). Rekonstrukcji tej dokonano w kategoriach analizy systemów (fig. 2—3), które uznano za adekwatne do opisu biocenoz kopalnych. Badana biocenoza składała się głównie z roślinożernych ślimaków i osiadłych ponad powierzchnią dna organizmów filtrujących (fig. 4). Ponieważ zaś luźny osad, w którym skamieniałości występują, czynił biotop niedostępnym dla morskich traw, mioceńską biocenozę łychowską zinterpretowano (*por.* Radwański 1977) jako makrobentos związany z wodorostami.