

$$\log_2(p_i) = 3.32 \cdot \log_{10}(p_i)$$

Calculated mean diversity value for the documented interval was 1.96; the oscillating values ranged by 0.4 (Q19, B15), and 3.6 (quadrat 20, bed 16) – Tab. 1.

2.2. Patchiness

A paradigm of two types of meadows exists. First type represents patchily arranged shrubs in mosaics, with more or less pronounced interspaces, whereas the second type is characterised by chaotic and very dense diffusion of the locations. Which type possess better capacity for the increase of diversity?

Patchy structure was evaluated from several aspects. One approach is emphasised here, that the number of isolated patches [tending to mosaics] was compared with number of interconnected and diffusive patches [tending to be random]. In practice, a ratio of total number of patches per 2 × 2 m quadrat to number of isolated patches was calculated. This ratio is here called uniformity. For correlation with other parameters, it was scaled by a logarithmic function:

$$U' = \log_{10}(N/N_s)$$

Calculated mean value was 0.69; observed minimum was at 0.11 (Q18, B14), maximum at 1.70 (Q28, B25).

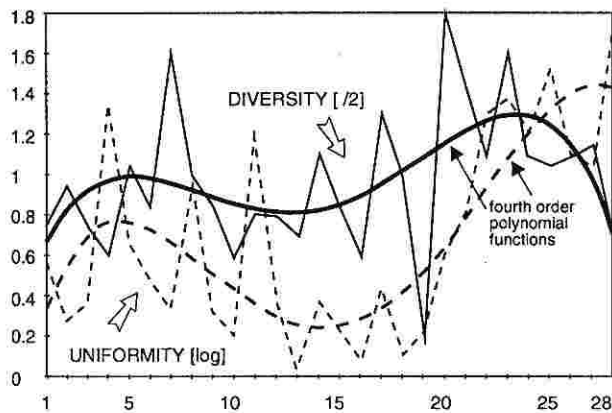


Figure 1. Development of the diversity and uniformity (patchiness) values in the section, numbers 1–28 mark the quadrats.

2.3. Relation between the both quantities

The sequence of data was smoothed by fourth order polynomial functions (Fig. 1). Both curves (diversity and uniformity) closely follow one another. An evident minimum (valley) developed simultaneously on the both curves between the Qs9 and 17 (B4 to 13, Tab. 1, Fig. 1). These conformable trends continue up to the Q21 (B17), however, beginning from this point, the trends gradually diverge. The diversity index intensively decreases while the uniformity strongly increases.

Although the coral – stromatoporoid carbonate ramp-type community was traced up to the Q25 (B20A), where it was replaced by a bacterial – poriferan one, the above mentioned splitting of trends began two sedimentary cycles before (B17). The splitting is interpreted as a result of the drowning of the ramp. It is clear now that this feature is not identical with the second-order sedimentary omission between the long-distance concordant beds 20A–20B, where the last stromatoporoid surface was slightly truncated and covered by bioclastic debris with phosphatic micro-nodules. The ecological signals started roughly 0.22 Ma before, if the assignment of the sedimentary cycles to 110 ka order is correct.

Generally, the diversity and uniformity are conformably developed in the coral – stromatoporoid ramp, including the minima of both quantities at and after the significant crisis of the biota in B4 – B5 (Čejchan and Hladil, in press, Tab. 1 herein). The higher the diversity is, the higher the uniformity is and vice versa. The conformity of these trends was broken before the coming onset of bacterial – poriferan benthos. For the deeper carbonate ramp environment, with many inhibiting factors (nodular and cephalopod limestone environment), just the opposite situation was typical: lower diversity coincides with higher uniformity and vice versa.

3. Relationship between the biomass production and coverage of seafloor

3.1. Biomass production

What was the true incremental part of soft body on the surface of clonal colony organisms? Calculating the biomass production was biased by many problems, particularly distinguishing between newly formed and pull-up biomass of clonal colony organisms. Some clonal colonies have poor signs of seasonal mortality or rejuvenations, and in these situations the proportion between newly formed and pull-up biomass must be estimated only on the basis of the best hypothesis. While these problems biased the data about the soft bodies, the skeletal tissue accretion was estimated by one-order higher fidelity. The biomass handled in this study cumulates both the skeletal and soft tissues. Units of this quantity are in [kg.m⁻².year⁻¹]. The lowest biomass production was 0.02 in Q15 (B11), the highest one was 4.89 in Q8 (B4). The mean biomass production was 0.90.

3.2. Coverage of the seafloor

Coverage of the surface is expressed as a number which ranged between 0 → 1. If occasionally values over 1 occurred, then the horizontally projected surface consisted of more levels (like microcaves). The number essentially represents the ratio of the covered surface to the all standard surface of 2 × 2 m quadrats. The number is dimensionless, as other ratios and indexes. The lowest coverage ratio was 0.13 in Q18 (B14), the highest ratios which exceed the value of 1 occurred on Q11 (B5) and Q28 (B25). The mean coverage ratio was 0.65.

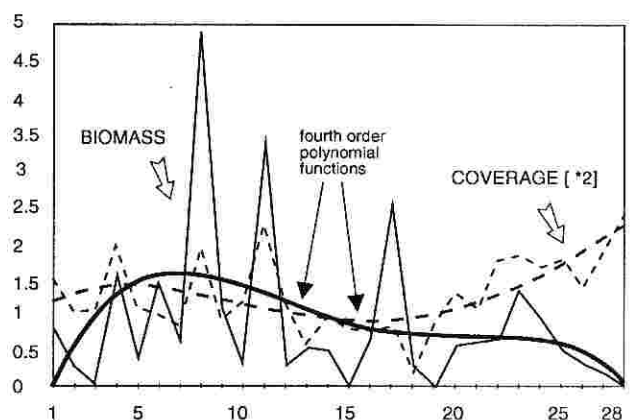


Figure 2. Development of the coverage and biomass values in the section.

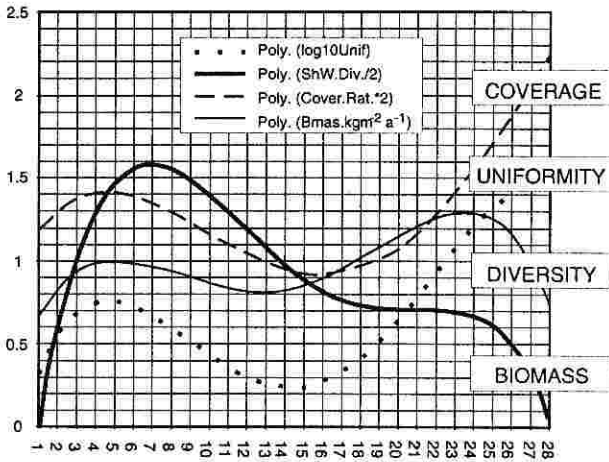


Figure 3. Comparison of four basic benthic colonisation parameters (diversity, patchiness, biomass production, coverage of seafloor), their development expressed by fourth order polynomial functions.

3.3. Relationship between the quantities

The biomass production of benthos increased until the Q8 (B4), from where it slightly but continuously grew weaker. A polynomial curve of the fourth order shows a slight valley between the Qs13 and 20 (B7 to 16), with a delay in comparison with the valley of diversity [Qs9 to 17 (B4 to 13)], Tab. 1 (Figs. 1 and 2). After a period of slower biomass production decrease at Qs21 to 25, the final trends of the curve declines.

The coverage ratio maintained moderately high values from the beginning of the curve (Fig. 2) but it reflected the post crisis syndrome by its depression between the Qs12 to 19 (B6 to 15). This valley is slightly shifted back in comparison with that of the biomass but forwards in comparison with that of the diversity (Fig. 3). Although this shift may contain some interpretable information, it seems biased by the low number of accessible quadrats (paleo-seafloors). Beginning from Q19, the coverage rises (Fig. 2). Mean sub-linear trend of this increase was stopped as soon as the maximum values near 1 were reached.

4. Comparison with the values known from Recent coral ecosystems

4.1. Occurrence of the positive shifting of the diversity peaks

This feature was described fifteen years ago (Sorokin 1993, after Colgan 1981). While the increase of diversity is relatively steep for undisturbed evolution of coral community cycles, the subsequent gradual decrease of the diversity needs more time (negative shift of the diversity peak). The cycle in conditions of periodical re-appearance of stress conditions shows, in an opposite way, a longer fluctuating period of rising diversity. After the occurrence of the diversity maximum, the subsequent decrease is much more steep than in the undisturbed case, with a trend to consequent collapse (positive shifting of the diversity peak).

When the reef system is traversed across facies (horizontally), the diversity peaks are usually present at the deeper reef margin (20 – 40 m of depth), i.e. around the proper margin of the reef ecosystem. Where stress

factors predominate, diversity in the interiors of the reef structures is the first to fail. Only rarely do such situations produce an opposite result. Comparison between the fossil and Recent diversity responses indicates similar rules. The magnitude of the Recent diversity peaks can reach values 3 – 4 of H' (Shannon-Wiener diversity index).

4.2. Values of the biomass, wet weight

The Recent values for coral reef macrobenthos vary between 0.002 and 3.2 $\text{kg}\cdot\text{m}^{-2}$ (cf. Sorokin, 1993). Including the microbenthos, the wet biomass can hardly exceed 5 $\text{kg}\cdot\text{m}^{-2}$, and average Recent values can be approximately estimated to ca. 0.35 $\text{kg}\cdot\text{m}^{-2}$. However, if seagrass is included, the biomass maximum values rise up to 22 kg, and means to 5 $\text{kg}\cdot\text{m}^{-2}$. Consequently, if the Recent benthos productivity can be estimated as 1/5 of total wet biomass, it can represent in average 0.07, and in maximum 1 $\text{kg}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ (average 1 kg, and in maximum 4.4 $\text{kg}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$). In comparison with Recent reef benthos production, the calculated Late Devonian values (average 0.9 kg, and maximum ca. 4.9 $\text{kg}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$) seem to be significantly higher, but they are quite similar to recent reefs with seagrass. Higher Devonian productivity of zoo-benthos may be related to increased productivity of the pelagic photic zone as recorded by the evident surplus of deposited organic matter in sediments. Common excessive values of productivity of fertilised seas correspond to numerous Late Frasnian – Early Famennian anoxic events when oxygen-depleted water levels were in direct contact with the reefs.

4.3. Coverage of the sea floor and its uniformity

Little data from recent reefs is available for comparison. Individual data about the cnidarian coverage from Red Sea (Schuhmacher et al. 1993) indicate that the Late Devonian coverage and uniformity do not differ significantly from the recent benthic systems.

5. Conclusions

5.1. Recovery with reconstruction of similar ecosystem

- (1) Coincident peaks of both benthic diversity and associated biomass production were documented during periods of sufficient recovery. Nevertheless, both quantities differed by overall trends after the passing through a serious crisis: while the biomass production displays generally a decreasing trend, the diversity reached its maximum just before the definite collapse of the structure tending to reorganisation into bacterial – poriferan high coverage but low productive communities.
- (2) The uniformity and coverage parameters displayed similar relationships. However, the trends to utilise all of the possible surface appeared with a slight delay. This usage probably restarted just after decay of the mosaic structure of the benthos.
- (3) The intensive Late Frasnian crisis of benthic communities evoked depressions in all studied parameters (diversity, biomass, coverage and uniformity). Slightly shifted settings of these valleys can be interpreted in terms of the following hypothesis: (a) first signal of recovery after the post-crisis depletion is a slight rise in diversity, (b) this first diversity increase was still related to isolated patches and mosaic structures,

whereas the uniformity of the carpet rose rather later, (c) strategies towards the higher coverage and to increased biomass productivity continued this recovery process.

5.2. Recovery with origination of completely different system

(1) Fatal extinction of relict coral – stromatoporoid assemblages was characterised by a pre-extinction peak of species diversity. Nevertheless, even during this last peak three trends are almost apodeictically con-

figured: rapid decrease of biomass production, decay of structures in favour of rising uniformity (i.e. decay of complicated mosaics), and attempts to spread in thin mottled films over the all accessible surface. These trends usually signalise the collaps of the ecosystem.

(2) This collapse / reshuffling of the benthic communities in Mokrá was incidentally reinforced by drowning of the ramp which was related to the changing character of the Early Famennian Horákov inlet. A couple of controversial trends of decreasing of biomass vs. increasing of coverage and decreasing of diversity vs. increasing of uniformity significantly marked this final decay of relict reef-related ecosystems.

Ser.No.Q.	Bed_No.	Markers	ShW.Div.	ShW.Div./2	Unif	log ₁₀ Unif	Cover.Rat.	Cover.Rat.*2	Biomass kgm ² a ⁻¹
1	-2		1.5	0.75	3.7	0.57	0.75	1.5	0.83
2	-1		1.9	0.95	1.9	0.28	0.53	1.06	0.31
3	0		1.5	0.75	2.3	0.36	0.54	1.08	0.06
4	1		1.2	0.6	22	1.34	0.97	1.94	1.56
5	1		2.1	1.05	4.6	0.66	0.56	1.12	0.43
6	2		1.7	0.85	3	0.48	0.51	1.02	1.46
7	3		3.2	1.6	2.2	0.34	0.43	0.86	0.65
8	4	▼	2	1	8.8	0.94	0.97	1.94	4.89
9	4	Crisis	1.7	0.85	2.1	0.32	0.47	0.94	1.12
10	5		1.2	0.6	1.6	0.20	0.59	1.18	0.36
11	5		1.6	0.8	15.3	1.18	1.13	2.26	3.37
12	6		1.6	0.8	2.3	0.36	0.59	1.18	0.34
13	7		1.4	0.7	1.1	0.04	0.29	0.58	0.55
14	8		2.2	1.1	2.3	0.36	0.5	1	0.51
15	11		1.7	0.85	1.8	0.26	0.41	0.82	0.02
16	12		1.2	0.6	1.2	0.08	0.38	0.76	0.67
17	13		2.6	1.3	2.7	0.43	0.43	0.86	2.53
18	14		2	1	1.3	0.11	0.13	0.26	0.33
19	15		0.4	0.2	1.7	0.23	0.45	0.9	0.02
20	16		3.6	1.8	4	0.60	0.65	1.3	0.58
21	17		2.9	1.45	6.5	0.81	0.55	1.1	0.64
22	18		2.2	1.1	19.5	1.29	0.88	1.76	0.68
23	19		3.2	1.6	23.5	1.37	0.91	1.82	1.33
24	20A	▼	2.2	1.1	16.5	1.22	0.84	1.68	0.98
25	20A		2.1	1.05	33	1.52	0.89	1.78	0.52
26	20A	Drown.	2.2	1.1	13	1.11	0.7	1.4	0.33
27	22		2.3	1.15	11	1.04	0.97	1.94	0.21
28	25		1.4	0.7	50	1.70	1.21	2.42	0.05

Table 1. Calculated values, quadrats 1–28. The prominent crisis ascends in the bed 5, quadrat 10; drowning is documented from the bed 20A, quadrat 26.

References

ČEJCHAN P. and HLADIL J. (in print). Searching for extinction / recovery gradients: the Frasnian-Famennian interval, Mokrá Section, Moravia, Central Europe. In Hart M.B. (ed.): *Biotic Recovery from Mass Extinction Events, Geological Society Special Publication*, 102, 135–161. London.

HLADIL J. and KALVODA J. 1993. Extinction and recovery successions of the Devonian marine shoals: Eifelian-Givetian and Frasnian-Famennian events, Moravia and Bohemia. *Věstník Českého geologického ústavu* [Bulletin of the Czech Geological Survey], 68 (4), 13–23.

HLADIL J., KREJČÍ Z., KALVODA J., GINTER M., GALLE A. and BEROUŠEK P. 1991. Carbonate ramp environment of Kellwasser time-interval (Lesní lom, Moravia, Czechoslovakia). *Bulletin de la Societe belge de Geologie*, 100 (1–2), 57–119.

MAY A. 1994. Ideas about interactions among the sea-level changings, biogeographic patterns, global

extinction events, and recovery – exemplified by the Devonian. *Geolines*, 1, 18–19. Praha.

RACKI G. 1990. Frasnian / Famennian event in the Holy Cross Mts, Central Poland: Stratigraphic and ecologic aspects. In Kauffman, E.G. and Walliser, O.H. (eds): *Extinction Events in Earth History. Lecture Notes in Earth Sciences*, 30, 169–181. Springer-Verlag, Berlin.

SCHINDLER E. 1990. The Late Frasnian (Upper Devonian) Kellwasser Crisis. – In Kauffman E.G. and Walliser O.H. (eds): *Extinction Events in Earth History. Lecture Notes in Earth Sciences*, 30, 151–160. Springer-Verlag, Berlin.

SCHUHMACHER H., KROLL D.K. and REINICKE G.B. 1993. Long-term fluctuations of coral communities at Aqaba and on Sanganer-Atoll (Northern and Central Red Sea) over a decadal period. In Piller W.E. (ed.): *Abstracts of the First European Regional Meeting, International Society for Reef Studies*, Vienna 93 (1), 61. Wien.

SOROKIN Y.I. 1993. *Coral Reef Ecology. Ecological Studies*, 102, 465 pp., Springer Verlag, Berlin.