Diversity, patchiness, biomass production, and coverage of seafloor: response to extinction-recovery processes

Jindřich HLADIL

Geological Institute, Academy of Sciences of the Czech Republic, Rozvojová 135, CZ – 165 02 Praha 6 – Lysolaje, Czech Republic, e-mail: lucie@gli.cas.cz

ABSTRACT. Benthic colonisations of Late Devonian (Frasnian – Famennian) carbonate ramps yield data about four overall ecological parameters: diversity, patchiness, biomass production, and coverage of the seafloor. The values and dynamics of these parameters are similar to the recent ones. Recoveries from non-fatal crises with successful reconstruction of coral – stromatoporoid communities were characterised by an increase in all parameters, in the following order: diversity > patchiness (uniformity) > biomass and coverage. Nevertheless, fatal extinction of the coral-stromatoporoid community was indicated by decrease of biomass production and increase of uniformity and coverage ca 0.22 Ma before the actual extinction, even before the last, pre-crisis peak of the benthos diversity.

KEYWORDS: colonisation, benthos palaeoecology, biological crises, Late Devonian.

1. Introduction

Limited survivorship of some relict shallow-water benthic communities after the global Kellwasser crisis has been recently studied in several places around the world (Alberta, Yunnan, Kazakhstan, Belorussia; cf. Hladil et al. 1991). These studies seem to be constrained due to the extraordinary catastrophic extinction aftermath of the event for the all shelf facies including the benthic communities of organisms. The shelves experienced strong sea-level drops (from 50 to 140 m), following overflows of anoxic and poisoned waters (Schindler 1990, Hladil and Kalvoda 1993). Rapidly shallowed vs. drowned sedimentary sequences gave rise to sedimentary starvation on exceptionally surviving carbonate ramps (Racki 1990, Hladil et al. 1991). Additionally, the beginning of orogenic collision caused the tilting of ramps toward the basins (in Variscan Europe). On the top of that, uniform cosmopolitan communities of Frasnian age were highly sensitive to such catastrophes as they possessed only limited reservoirs for eventual recovery (May 1994).

One of the investigated localities is in Moravia (Mokrá section). Although discussion about the exact placement of the Frasnian – Famennian boundary in the section continues (Čejchan and Hladil, in press), the data sets related to this F – F section are remarkably large and they provide a good possibility for consequent studies. Especially, the reconstructed quadrats of paleo-seafloors, presented at the Plymouth 1994 IGCP 335 conference, involve information which can be viewed in terms of general ecological parameters. Mokrá W-quarry Section profiles one of the facies rock segments which were tectonically stacked at the southern closure of the Moravian Karst. This segment represents the proximal part of a carbonate ramp that developed from the late Devonian inlet of the Rhenish – Ukrainian seas. The best correlation for the facies pattern (Horákov embayment) is fit to dimensions of 100 km with the maximum depths of ca 500 m (Hladil et al. 1991). This inlet provided a shelter to Late Frasnian benthic survivors until the early / middle Famennian tilting of the ramp, with general on-shore approaching pelagic influences, definitely overruled all the relict configurations (*Pa. crepida* Zone).

The data involved in this study are related to a 6 m thick strata sequence, which consists of 25 beds and 28 quadrats (Tab. 1).

2. Relationship between diversity and patchiness

2.1. Diversity of benthos

Problem of individuality suggests many problems (e.g., what is an individual?), or multiple layering of genetic, reproductive, and behavioural organisations.

The seafloor was settled by organisms of different construction and some of these constructions create problems for definition of individuality. Types of construction were represented, for example, by (a) solitary individuals (benthic foraminifers, gastropods, brachiopods), (b) clonal colonial organisms (stromatoporoids – *Tienodictyon*, *Labechia*; tabulates – *Scoliopora*, *Aulostegites*), (c) retrocolonies (i.e. typical colonial organisms regressed to solitary forms; amphiporids, rugose corals – *Tabulophyllum*), and (d) modular organisms of various kind (bacterial, algal, and poriferan clusters / colonies / individuals).

The main problem is that organisms of group (a) grew often in self-regulated patches like dense micropopulations which tend to differ one from the other. Group (b) is characterised by connective tissues. These clonal colonial organisms were differentiated in various stage, from poor individuality (*Labechia*) to obvious individuality (*Aulostegites*). Reduction of the clonal colony development to pseudo-solitary individuals, e.g. *Amphipora*, (c) was not accompanied by re-appearance of standard solitary strategies – the distribution on the seafloor and life reactions resemble more a speckled colony type than any simple solitary one. Modular organisms of different levels (d) form amoeboid more or less fixed clusters / colonies / individuals.

For the purpose of diversity mapping (Čejchan and Hladil, in print) the classic individual concept completely failed, as the "individuals" were usually irrelevant either in their proper definitions or in the interactions with the neighbourhood. For that reason, the surface of the one-taxon-patches was cumulatively recorded in square decimetres. This non-standard unit [dm^2 of active surface] was used in place of the standard individuals usually considered in the benthic ecology.

Calculations of diversity were based on the Shannon – Wiener index (H'):

$$H' = -\Sigma^{s}{}_{i-1}\,[p_i \,.\, \log_2(p_i)]$$
$$p_i = N_i / N$$

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

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).

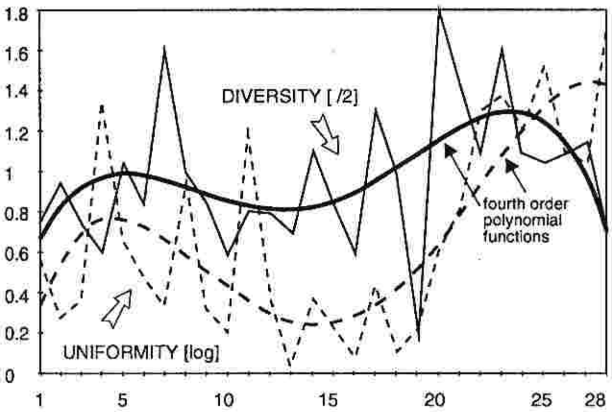

Figure 1. Development of the diversity and uniformity (patchiness) values in the section, numbers 1–28 mark the quadrats.

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 – stromatoporiod 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.

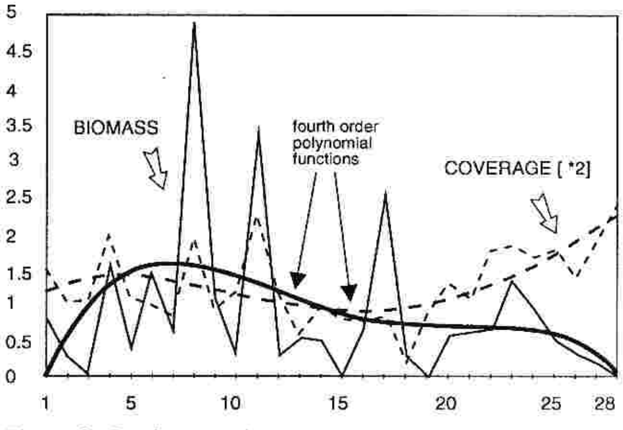

Figure 2. Development of the coverage and biomass values in the section.

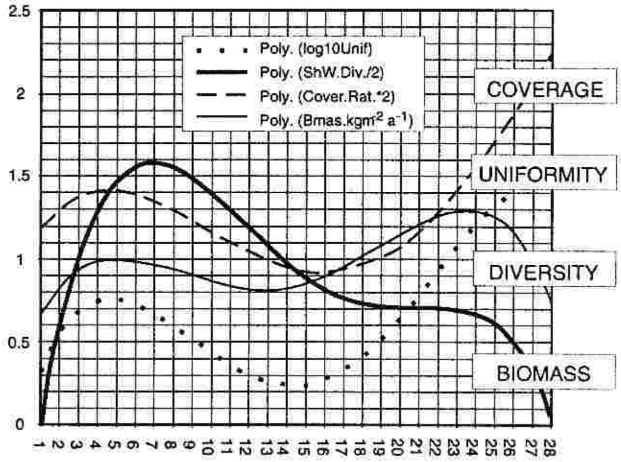

Figure 3. Comparison of four basic benthic colonisation parameters (diversity, patchiness, biomass production, coverage of seafloor), their development expressed by fourth order polynomial functions.

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 kg.m^{-2} (cf. Sorokin, 1993). Including the microbenthos, the wet biomass can hardly exceed 5 kg.m^{-2}, and average Recent values can be approximately estimated to ca. 0.35 kg.m^{-2}. However, if seagrass is included, the biomass maximum values rise up to 22 kg, and means to 5 kg.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 kg.m^{-2}a^{-1} (average 1 kg, and in maximum 4.4 kg.m^{-2}a^{-1}). In comparison with Recent reef benthos production, the calculated Late Devonian values (average 0.9 kg, and maximum ca. 4.9 kg.m^{-2}a^{-1}) seem to be significantly higher, but they are quite similar to recent reefs with seagrass. Higher Devonian productivity of zoobenthos 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 configured: 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.

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