Relationship among sea-level fluctuation, biogeography and bioevents of the Devonian: an attempt to approach a powerful, but simple model for complex long-range control of biotic crises

Andreas MAY

Geologisch-Paläontologisches Institut, Correnssstr. 24, D-48149 Münster, Germany (Private address: Friedrich-List-Str. 66, D-59425 Unna, Germany).

ABSTRACT. Connections among changing sea-level, development of marine biogeography and appearance of bioevents in Devonian times are emphasised. Decreasing Devonian provincialism of the marine fauna reflects rising sea-level of global ocean. Whereas the Emsian sea-level lowstand was accompanied by strong provincialism of the marine communities, the Frasnian highstands were linked to an unusual decrease of provincialism. As generally documented, the partial but intensive transgressional events (often related to bioevents) were usually associated with a decrease of the provincialism. The best explanation for the majority of Devonian bioevents is the effect of oceanic anoxia. A model suggested herein operates with a fast transgression related to fast ocean sea-level rise. A direct consequence of this fast transgression was the increased primary biomass production (caused by both increased influx of nutrients and increased total surface of shallow seas). Decreased oxygen supply of oceans continued this process being caused by the global temperature increase which resulted from the albedo decrease. These consequences of these combined factors produced an oceanic anoxic event which started the extinction processes of the bioevent. The well-documented pattern of intensified biological crises during the Devonian, time-slice by time-slice (from Emsian to Frasnian), is explained as a direct result of decreased provincialism of the marine fauna. Both decrease of the provincialism and increased intensity of the Devonian bioevents can be deduced directly or indirectly from changes of global sea-level. This simply constructed but very complex explanation yields two advantages: first, it needs only very few influencing factors; second, it can basically renounce incalculable influences (e.g. meteorite impacts). The suggested concept of oceanic anoxic events can explain also other major bioevents of the Earth history.

KURZFASSUNG: Der Artikel versucht, Zusammenhänge zwischen den Veränderungen des Meeresspiegels, der Entwicklung der marinen Biogeographie und den Bioevents im Devon herauszuarbeiten und zu erklären. Die Entwicklung des Faunen-Provinzialismus im Devon ist ein Ergebnis der Entwicklung des globalen Meeresspiegels. Im Emsium war der Meeresspiegel niedrig und der Provinzialismus der Meeresfauna gross, im Frasnium war der Meeresspiegel hoch und der Provinzialismus sehr gering. Insbesondere einige Trangressions-Schübe, die sich auch als Bioevents bemerkbar machten, führten zu schnellen Abnahmen der Grösse des Provinzialismus. Die beste Erklärung für die meisten devonischen Bioevents ist das Auftreten von ozeanischen anoxischen Events. Das hier vorgestellte Modell setzt bei schnellen Transgressionen an, die durch schnelle Meeresspiegel-Anstiege verursacht wurden. Die Konsequenzen einer schnellen Transgression waren gesteigerte Primärproduktion organischer Substanz und geringere Sauerstoff-Versorgung der Ozeane, was zusammen zum ozeanischen anoxischen Event und zum Bioevent führte. Der Umstand, dass die Intensität der Bioevents vom Emsium zum Frasnium zunahm, wird durch die Abnahme des Provinzialismus der Meeresfauna in dieser Zeit erklärt. Sowohl die Entwicklung des Provinzialismus der marinen Fauna als auch das Auftreten und die Intensität der Bioevents im Devon lassen sich direkt oder mittelbar aus der Entwicklung des globalen Meeresspiegels ableiten. Dieser sehr umfassende Erklärungsansatz hat den Vorteil, mit sehr wenigen Einflussfaktoren auszukommen und auf unkalkulierbare Einwirkungen (wie z.B. Meteoriten-Einschläge) völlig verzichten zu können. Vermutlich ist das hier entwickelte Konzept eines ozeanischen anoxischen Events auch auf andere Bioevents übertragbar.

KEYWORDS: Devonian, Kellwasser Event, ecosystems, biogeography, sea level fluctuation.

1. Introduction

Within the Upper Devonian, one of the biggest extinction events of Earth history occurred which was less important than the Permian/Triassic boundary extinction but evidently more important than the Cretaceous / Tertiary boundary extinction (Boucot 1990a: 22). This bioevent, called Frasnian / Famennian Event or Kellwasser Event, affected intensively the whole shallow marine fauna and extinguished the mid-Palaeozoic reefs abruptly. Consequently, for the last twenty five last years many publications have dealt with the Kellwasser Event, but a consensus about the causes has not been obtained. Instead it has been discovered that before the Kellwasser Event, other similar Devonian perturbations occurred, which did not cause catastrophic extinctions. Two questions arise from these two facts:

(1) What were the causes of the Devonian bioevents?

(2) Why was the intensity of the Devonian bioevents prior to the Kellwasser Event significantly smaller than the effect of the Kellwasser Event? This paper, based on a German paper by May (1996), is an attempt to answer these questions. It seeks to show the causality among the changings of the sea-level, development of marine biogeography, and bioevents within the Devonian.

2. Palaeobiogeography

The Kellwasser Event was determined by evolution (and spatial extension) of the marine biogeographical units during the Devonian. It can be documented best by brachiopods as they represented one of the most important groups of the shallow marine benthos: the world-wide diversity of brachiopods climaxed in the Emsian with 225 genera and decreased from stage to stage down to 93 genera by Frasnian times (Boucot 1975: 90, Fig. 22A). Compared with this, the further decrease to 80 genera during the Famennian was relatively modest. Consequently, we have to go back to the Emsian, if we want to understand the historical concept of the Kellwasser Event.

New Emsian marine biogeography exhibits the following three faunal realms (e.g. Boucot 1975: 140–144; 1988; Oliver 1976): (1) the Malvinokaffric Realm of the Gondwana continents with cool water, (2) the subtropical Eastern Americas Realm of the eastern North America and northern South America, and (3) the subtropical to tropical Old World Realm, reaching from western North America over Tasmania and Asia to Europe and North Africa. These three realms can be discerned very clearly by the distribution of brachiopods (e.g. Boucot 1975; Johnson 1979) and corals (e.g. Oliver 1976; Oliver and Pedder 1979; Hill 1981: 54–57; Pedder and Oliver 1990), but can be recognised also by the distribution of gastropods (Blodgett et al. 1990), stromatoporoids (Stock 1990), and trilobites. The barriers between these three realms are of different types. The barrier between the Malvinokaffric Realm and the others was climatic, because the water was cooler (Boucot 1988). Despite the relatively large climatic gradient (from the tropics to the poles) within the Emsian, there is no evidence for glaciers or a polar ice cap (Boucot and Gray 1982: 193–194, 196; Boucot 1988: 221). The western boundary of the Eastern Americas Realm was built by the Transcontinental Arch, and its eastern boundary by the active Appalachian Orogenic Belt (Ziegler 1988: 21, Fig. 4).

The Emsian had the highest level of provincialism of the whole Devonian (Boucot 1988: 211–212, 219; Oliver 1976: 370; Pedder and Oliver 1990: 267; Oliver and Pedder 1994: 185). Consequently, in this stage the world-wide number of brachiopod genera reached its maximum (Boucot 1975: 90, Fig. 22A). With the beginning of the Middle Devonian, the level of provincialism decreased more and more, caused by the beginning of transgressions (Johnson 1979; Oliver and Pedder 1979; Hill 1981: 484–485; Boucot 1988; Blodgett et al. 1990).

Very important for understanding these patterns is the curve of eustatic sea-level changings worked out by Johnson et al. (1985) and slightly improved by Johnson and Sandberg (1988). Figure 1 shows this curve. In the Lower Emsian, sea-level had its Devonian low, and in the Upper Frasnian – at the time of the Kellwasser Event – sea-level had its Devonian high. Comparing the sea-level curve with the diversity of brachiopods (Boucot 1975: Fig. 22A), it can be seen immediately that an inverse relationship exists. This is easily understandable, because a world-wide higher sea-level inundates hitherto existing barriers against faunal exchange. Furthermore, an increased sea-level causes a world-wide warming and more equalised climate.

Both of these processes, simultaneously caused by the transgressions, resulted in the state that in the Frasnian the shallow marine benthos in North America, Europe, Asia, and Australia was more or less uniform and had a tropical character. Indeed, this decrease of provincialism produced a (short-term) increase of diversity in a given area. However, due to the increased competition a decrease of global diversity resulted. A big part of the reduction of faunal diversity from the Emsian to the Frasnian can be explained by the increased competition alone. There are many examples for the decrease of diversity and the increase of geographical distribution from the Emsian to the Frasnian. I only want to refer to the investigation of ramose tabulate corals from northern Spain by May (1993, 1995).

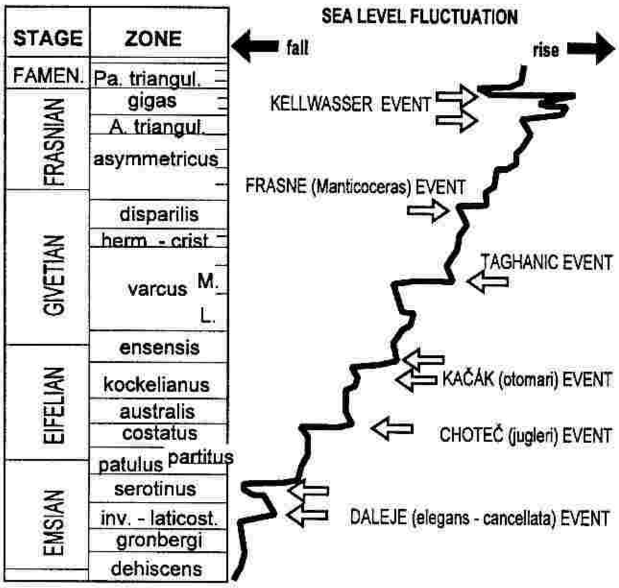

Figure 1. Sea-level curve from the Emsian to the Frasnian (after Johnson and Sandberg 1988: Fig. 1) with the stratigraphical positions of the bioevents.

3. Bioevents from Emsian to Frasnian

The bioevents of the Emsian to Frasnian have important properties in common: These events are developed typically in the **Hercynian magnafacies** (= Bohemian facies) of the outer shelf and basin. Here they are characterised by widely distributed black shales and/or black limestones, without benthos, but with ± rich pelagic fauna of ammonoids, tentaculitids and *Buchiola*-like bivalves. Remarkable extinction events and / or radiation events are connected with these black horizons (e.g.: Walliser 1985: 405, Fig. 1). Information about the impacts of the events on ammonoids are given by House (1985) and Becker and House (1994b), and information about trilobites are given by Chlupáč (1994). Furthermore, these bioevents coincide always with times of a rapid eustatic rise of sea-level (Fig. 1). The development of the bioevents in the Barrandian is documented by Chlupáč and Kukal (1986, 1988) in detail. In the following part, a brief summary of the bioevents is given.

3.1. Daleje Event

The Daleje Event, also called *elegans-cancellata* Event, is at the turn from the Lower Emsian to the Upper Emsian. It is known from different parts of Europe, Asia, North America, northern Africa, and Australia (Chlupáč and Kukal 1986: 172–173; Talent et al. 1993: 143; Becker and House 1994b: 82–90). In the Barrandian it is documented by a continuous increase in the amount of black shales or deep-water limestones (Chlupáč and Kukal 1986: 171–172; 1988: 122). The impact on the fauna is visible, but relatively weak. The stratigraphical position of the Daleje Event coincides with a strong sea-level rise in the *Polygnathus inversus* conodont Zone, but possibly also a little later with an increased rate of sea-level rise within this event (Fig. 1).

In the neritic sediments of the Rhenish Massif the Daleje Event is documented by the sand sedimentation of the Emsquarzit, which marks a transgression and shows a faunal change (Mittmeyer 1982: 265). At the time of the Emsquarzit the brachiopod genus *Paraspirifer* Wedekind

1926 developed from its ancestor *Brachyspirifer* Wedekind 1926, followed by a rapid radiation and an acme (Solle 1971). In Europe, *Paraspirifer* became extinct abruptly at the Choteč Event.

3.2. Choteč Event

The Choteč Event, also called *jugleri* Event, happened during the *Polygnathus costatus costatus* conodont Zone of the lower Eifelian, and therefore ± in the interval of a strong sea-level rise (Fig. 1). But the allocation is not fully certain, since the data of Chlupáč and Kukal (1986: 173) and Weddige (1988: 106) point to the lower *costatus* Zone, the data of Weddige (1988: 105) and Struve (1990: 261) indicate the higher *costatus* Zone, but Johnson et al. (1985: Fig. 12) and Johnson and Sandberg (1988: Fig. 1) allocate the sea-level rise to the end of the *costatus* Zone. The Choteč Event has been found in Europe, the Ural Mts., and Northern Africa (Chlupáč and Kukal 1986: 174; Becker and House 1994b: 83–90, 107–108). In the Barrandian this level is represented by an onset of dark coloured limestones and shales (Chlupáč and Kukal 1986: 174). The Choteč Event caused visible, but not serious changes in the trilobite fauna (Chlupáč 1994: 493).

In the Rhenish magnafacies, the Choteč Event can be recognised by the extinction of the upper Emsian to lower Eifelian OCA brachiopod fauna (Weddige 1988: 105–106; Avlar and May 1996). The OCA brachiopod fauna consists of *Uncinulus orbignyanus* (Verneuil), *Paraspirifer cultrijugatus* (C.F. Roemer), and *Alatiformia alatiformis* (Drevermann) and their variants (Struve 1982a: 405–406). This fauna and its abrupt extinction is documented from many parts of Europe from Spain to Poland (Struve 1982b: 433; García-Alcalde 1995: 24–25). In Europe, *P. cultrijugatus*, the last European *Paraspirifer* species, became extinct in the *costatus* Zone, but during the same time in North America, a similar species occurred abruptly (Johnson 1979: 293–294, Fig. 2). This species, called *Paraspirifer acuminatus* (Conrad) (cf.: Solle 1971: 137–140), was extinguished by the Kačák Event (cf. Johnson 1979: Fig. 2). This ambiguity of the Choteč Event, to cause simultaneously extinction and dispersal, is a characteristic feature of most Devonian bioevents.

The investigations of Avlar and May (1996) in the Lower Eifelian of the north-eastern Rhenish Massif show that the corals and stromatoporoids were not affected by the Choteč Event, but demonstrate a remarkable continuity during the whole Eifelian.

3.3. Kačák Event

The Kačák Event, also called *otomari* Event, took place during the Upper Eifelian, at the turn from the *Tortodus kockelianus* conodont Zone to the *Polygnathus ensensis* conodont Zone (cf. Walliser 1985: 403; Becker and House 1994b: 110), and coincides with a strong sea-level rise (Fig. 1). Localities showing the Kačák Event are known from Europe, Asia, northern Africa, North America, and Australia (Chlupáč and Kukal 1986: 177, 1988: 130; Truyóls-Massoni et al. 1990; Hladil and Kalvoda 1993: 14–19; Talent et al. 1993: 144–148; Becker and House 1994b: 85–91, 107–108). In the Barrandian the Kačák Event was very intensively expressed by the abrupt onset of black shales and it caused significant changes in the trilobite fauna (Chlupáč 1994: 495).

In the Rhenish magnafacies of the Sauerland (north-eastern Rhenish Massif) the Kačák Event is documented by the dark shales of the Oderhausen Beds, which can be traced lithostratigraphically into delta sediments (cf. May 1986: 30–33). May (1986: 30–33) paralleled the Oderhausen Beds from the Sauerland with the middle to upper part of the Junkerberg Formation from the Eifel (cf. Struve 1992: 522–523). After accepting this parallel, the following patterns result: With the Kačák Event occur for the first time representatives of two spriferid genera of eastern North America in the Rhenish Massif – the groups of *Spinocyrtia (Spinocyrtia) ostiolata* (Schlotheim 1820) and of *Mucrospirifer diluvianus* (Steininger 1853) (see Struve 1982b: 439). A short time later the spiriferids *Acrospirifer (Arduspirifer)* Mittmeyer 1972, *Subcuspidella* Mittmeyer 1965, *Struveina* Boucot 1975, *Vandercammenina* Boucot 1975, and *Rhenothyris* Struve 1970 died out (May 1986: 47; 1989). In the Lower Devonian and Eifelian of the Rhenish Massif, these five genera have significant biostratigraphical value. Except of a few immigrant brachiopods, no conspicuous faunal influx from the Eastern Americas Realm is evident. As an example, in the coral fauna of the lowermost Givetian from the north-western Sauerland, there are no traces of a remarkable faunal exchange with North America (May 1996: 331–332, Fig. 3).

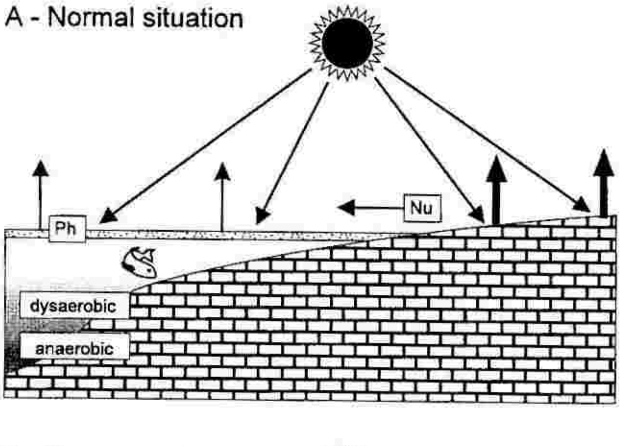

Figure 2. Sketch of the presented model for the rise of an oceanic anoxic event in the Devonian. Ph = phytoplankton; Nu = nutrients.
A – Normal situation: Relatively high albedo and small influx of nutrients, therefore little growth of phytoplankton and relatively deep upper margin of dysaerobic to anaerobic bottom water.
B – Rapid transgression: Increased shallow marine areas, decreased albedo, and large influx of nutrients, therefore decreased oxygen supply of the oceans and strong growth of phytoplankton resulting in a high upper margin of dysaerobic to anaerobic bottom water.

Much larger was the impact of the Kačák Event on the Malvinokaffric Realm, because this transgression caused a geologically sudden lowering of the global climatic gradient and a world-wide warming. These climatic changes extinguished the characteristic faunal elements of the Malvinokaffric Realm and therefore caused the end of the Malvinokaffric Realm (Boucot 1988: 221; 1990b: 128). However, it should be noted that there is no conspicuous transgression or anoxic event is known from the Malvinokaffric Realm at this time (written communication from A.J. Boucot, 10.1.1995).

In the Eastern Americas Realm, the Kačák Event made itself strongly felt by the immigration of faunal elements of the Old World Realm into the Eastern Americas Realm, which reinforced the extinction of endemic groups of the Eastern Americas Realm. This can be demonstrated with brachiopods (Boucot 1988: 214; Johnson 1979: Fig. 2) and with corals (Sorauf 1989: 333; Oliver 1990: 175; Oliver and Pedder 1994: 187–188).

3.4. Taghanic Event to Lower Frasnian

The prominent sea-level rise in the middle *Polygnathus varcus* conodont Zone (Fig. 1), known as under the name Taghanic Onlap (Johnson 1970), coincides with a major bioevent, called the Taghanic Event. It caused increased extinction rates within conodonts, brachiopods, trilobites, and ammonoids (Bayer and McGhee 1989: Fig. 3; Chlupáč 1994: 495; House 1985: 18; Becker and House 1994b: 112).

Remarkably, the Taghanic Event coincides only very rarely with a black shale horizon. Only from Morocco there is an occurrence of a thin, dark styliolinid shale horizon documented (Becker and House 1994b: 88, 112). Possibly, during the Taghanic Event the sea-level rose more slowly than in the previously discussed events (cf. Johnson 1970: 2078), so that the oceanographic requirements for a black shale horizon developed only for a very short time or only regionally (cf. chapter 4.3. herein).

The Taghanic Event had its largest impact in Northern America, because the transgression inundates the Transcontinental Arch, the barrier between the Old World Realm and the Eastern Americas Realm (Johnson 1970: 2078–2080). The disappearance of this barrier allowed the immigration of the fauna of the Old World Realm, which caused increased competition in North America. Consequently, many important taxa of North American origin became extinct, and the Eastern Americas Realm ceased (Boucot 1990b: 129; Sorauf 1989: 333; Oliver 1990; Oliver and Pedder 1994). After the Taghanic Event, the North American benthic fauna was dominated by taxa of the Old World Realm or of cosmopolitan character.

On the Gondwana continents, the Taghanic Event made itself felt by the extinction of the last remains of the former Malvinokaffric Realm (e.g. the trilobite *Metacryphaeus*, Boucot 1990b: 129; Chlupáč 1994: 495). Even in the Old World Realm the Taghanic Event is indicated by faunistic changes. After the disappearance of the barrier some brachiopods and corals of eastern North America were able to spread into the Old World Realm. An example is the solitary rugose coral *Siphonophrentis*, a typical faunal element of eastern North America. In the Upper Givetian this genus occurs very rarely in central and western Europe, e.g. in the Sauerland (May 1994: 157, Fig. 6.1).

In summary, it can be stated that the Taghanic Event was responsible for the decrease of the level of provincialism to zero in the Frasnian. This was done by the transgression and by the associated lowering of the climatic gradient. The main reasons for the extinction are: (1) the increased competition (see, e.g. Johnson 1979: 299) and (2) the disturbance of the hitherto existing synecological relations by the faunal migration. This is substantiated by the fact that immediately after the Taghanic Event – still in the middle *varcus* Zone (Ebert 1993: 51) – a phase of increased extinction began. The date of the climax of extinction differed between taxonomic groups (Ebert 1993: 51–57). The phase of increased extinction, which furthermore was characterised by an increased number of short-ranging species and genera (Ebert 1993: 49–52), ceased at the turn from the Lower to the middle *Polygnathus asymmetricus* conodont Zone. After this time the now typical Upper Devonian fauna returned to a pattern of slower changes.

Within this phase of increased extinction only one further bioevent can be extracted: the Frasne Event, also called Ense Event, which occurred in the lowermost *asymmetricus* Zone [= early *falsiovalis* Zone of Ziegler and Sandberg (1990)]. In this time widely distributed black shales were deposited (e.g. Walliser 1985: 404–405; Ebert 1993: 10, 19–21), beginning with the lowermost *asymmetricus* Zone and coinciding with a strong sea-level rise (Johnson et al. 1985: Fig. 12; Johnson and Sandberg 1988: Fig. 1; Ebert 1993: 27). The Frasne Event is clearly visible in the ammonoid fauna (House 1985: 19; Becker 1993a: 134–135).

3.5. Kellwasser Event

The Kellwasser Event, one of the most important extinction events in earth history, occurred in the uppermost Frasnian (Fig. 1). Its typical development, documented world-wide (e.g. Schindler 1990; Buggisch 1991: 55–56; Becker 1993a: 136–140; Becker and House 1994a), consists of two horizons of black limestones with very abundant fossils of pelagic organisms, but without benthos, and consequently is interpreted as being sedimented in an anaerobic (or dysaerobic) environment. It is important to recognise that each Kellwasser Horizon was the result of an independent event.

The first Kellwasser Event, producing the lower Kellwasser-limestone horizon, happened in the upper part of the lower *Palmatolepis gigas* conodont Zone, simultaneously with a very strong sea-level rise, which resulted in the highest sea-level of the whole Devonian. After that, sea-level fell distinctly. A short time later, in the uppermost *Palmatolepis gigas* conodont Zone [= *Palmatolepis linguiformis* Zone of Sandberg et al. (1988: 270)], sea-level rose again to a similar level, producing the upper Kellwasser-Limestone horizon. After this, at the beginning of the Famennian (Klapper et al. 1993), sea-level fell very strongly.

Becker and Feist et al. (1989) and Schindler (1990; 1993) demonstrate that no abrupt extinction occurred. In stead, a long-term, step-wise extinction, running over 1 – 2 million years from the beginning of the lower Kellwasser Event to the end of the upper Kellwasser Event is documented. This is supported by data of Klapper et al. (1993), Goodfellow et al. (1988), Becker (1993a: 136–140), Becker and House (1994a), McGhee (1990), Racki (1990) and other publications. A comparison of the fauna before the lower Kellwasser Event with the fauna after the upper Kellwasser Event shows that 60 – 75 % of the marine taxa died out (Boucot 1975: 125; Schindler 1990: 26; McGhee 1994: 514). Among others, the big Devonian stromatoporoid-coral reefs and their dwellers were extinguished (Stearn 1987; Cockbain 1989; Schindler 1990; Fagerstrom 1994). Throughout the Famennian, benthic faunas were impoverished, showing overall low diversity (Boucot 1990a: 16; 1994: 30) as a consequence of the Kellwasser events.

It is important to consider, which ecological groups were affected very seriously by the bioevent and which were only slightly affected. A review of the literature (e.g. McGhee 1982; Sorauf 1989: 328–329; Schindler 1990: 26–33; Klapper et al. 1993; Chlupáč 1994: 495; Fagerstrom 1994; Oliver and Pedder 1994: 186) shows that the shallow marine benthos fauna (e.g. brachiopods, corals) was severely affected but the benthos of the basins and the fauna of marginal marine areas were affected only slightly. Concerning the pelagic groups, the situation is non-uniform, some were seriously affected, other not. The flora were not affected by the Kellwasser Event, as can be demonstrated by the calcareous algae (cf. Fagerstrom 1994: 181, 183) and with the terrestrial flora (Copper 1986: 838).

4. Explanation of the Kellwasser Event and the previous bioevents

Many hypotheses have been developed to the mass extinction at the Kellwasser Event. If someone wants to check, which of these hypotheses give a conclusive explanation, he must compile at first a catalogue of criteria, which are crucial for any hypothesis. Such a catalogue, derived from the data of this paper, is given below.

4.1. Crucial criteria for the explanation of the Kellwasser Event

Any conclusive explanation for the Kellwasser Event must account the following facts:

(1) The Kellwasser Event is not a singular event, but consists of two brief successive events, which produced the mass extinction by their interaction.

(2) Before the Kellwasser Event occurred, similar bioevents had a weaker impact on the fauna. These bioevents should have comparable causes.

(3) The Kellwasser Event and the previous similar bioevents always coincided with a rapid sea-level rise and the occurrence of anoxic sedimentation.

(4) The extinction at the Kellwasser Event occurred not abruptly, but within a certain period. Furthermore, the extinction shows decoupling in that certain environments (or ecosystems) were affected more seriously than others. The shallow marine benthic fauna was affected most seriously. These phenomena can be seen also by the previous bioevents, but in a weaker manner.

(5) In the considered period from the Emsian to the lower Famennian there are no indications of the occurrence of an ice cap or a glaciation (Boucot and Gray 1982: 193–194, 196; Boucot 1988: 221–223; Becker and House 1994a: 68; May 1996: 336).

4.2. Previous models for the explanation of the Kellwasser Event

Most previous models have assumed the following reasons: (a) impact of an extraterrestrial body (meteorite), (b) cooling, (c) warming, (d) regressions and / or transgressions, and (e) anoxic events. These models will be checked against the catalogue of criteria outlined above.

(a) **Impact of an extraterrestrial body (meteorite):** McGhee (1982: 498), Playford et al. (1984), Sandberg et al. (1988: 296–297), Claeys et al. (1992) and other authors postulate that the mass extinction was caused by the impact of a meteorite. However, the iridium anomalies and / or microtektites (or glass spherules) found by Playford et al. (1984), McGhee and Orth et al. (1986), Wang and Bai (1988), Wang and Orth et al. (1991), Nicoll and Playford (1993), and Claeys et al. (1992, 1994) have different ages in the lower Famennian (*triangularis* Zone to *crepida* Zone) and therefore are younger than the Kellwasser Event (see, e.g. McGhee and Orth et al. 1986; Wang and Bai 1988; Becker and House et al. 1991: 185; Nicoll and Playford 1993; Claeys et al. 1992, 1994; McGhee 1994). Furthermore, a part of these iridium anomalies surely was caused by microbial (or geochemical) enrichment processes and there is a high probablity that the remaining findings were also caused in this way (see e.g. McGhee and Orth et al. 1986: 779; Orth et al. 1990: 48–49; Hurley and Van Der Voo 1990; Wang and Orth et al. 1991: 779; Nicoll and Playford 1993). Consequently the reported iridium anomalies and microtektites are no proof of a meteorite impact. Additionally, it would be very difficult to explain items (1) to (4) with a meteorite impact. The decoupling phenomenon is an especially significant counter-argument (cf. Boucot 1990a: 21–22).

(b) **Cooling:** Several authors [e.g. Copper (1986), Stanley (1987: 73, 79–89), Sorauf (1989: 337), and Schindler (1990: 98)] assume that a cooling or glaciation triggered by the collision of Laurussia and Africa is the reason for the Frasnian/Famennian extinction. This model conflicts with item (5) and does not explain the items (1) to (3). Instead of cooling, the water temperature was actually relatively high (Thompson and Newton 1988; Brand 1989). Furthermore, the collision between Laurussia and Africa did not preceed the Famennian (cf. Raymond et al. 1987; Ziegler 1988: 32; Becker 1993b).

(c) **Warming:** Thompson and Newton (1988) and Brand (1989: 319–326) explain the Kellwasser Event by an increased temperature of ocean water. It is important to point out that the temperatures deduced by Brand (1989) from the (δ^{18}O data are doubtful because of reasons discussed by Brand (1989: 319–322). Another counter-argument is that the faunas should have been able to survive in higher latitudes, if the water temperature increased too much in the lower latitudes.

(d) **Regressions and/or transgressions:** These processes are proposed as the causes of the mass extinction by Johnson et al. (1985: 581), Johnson and Sandberg (1988: 175–177), Johnson (1990: 930), Hladil et al. (1986), and Hladil and Kalvoda (1993: 22). This alone cannot explain the remarkable coincidence with anoxic sedimentation. Furthermore, the question remains, as to the extinction happened. A serious decrease of the shallow marine area must not occur necessarily; and it is an open question as to whether the stress of shifting area alone can cause a mass extinction.

(e) **Anoxic events:** Wilde and Berry (1984, 1986) explained extinction events by models of oceanic overturn. Especially important in these models is the rapid mixing of anoxic deep sea water and shallow sea water during the change between times without polar ice caps and times with polar ice caps, which may cause an anoxic event. The anoxic oceanic overturn model of Wilde and Berry (1984, 1986) has been adopted – unmodified or modified – by several authors (e.g. Wilde and Berry 1984: 158-159; Schindler 1990; Buggisch 1991: 49, 64–67; Joachimski and Buggisch 1993: 677–678; Becker 1992; Becker 1993a, b; Becker and House 1994a) to explain the Kellwasser Event and other Devonian bioevents. These models explain very well items (1) to (4), but cannot be reconciled with item (5), the absence of glaciation. There is no evidence for an oceanic cooling (cf. Thompson and Newton 1988; Brand 1989). Only the model of Becker and House (1994a: 68–69) does not depends on an initial cooling, but it can be rejected on the basis of reasons discussed by May (1996: 339).

In other variation, Geldsetzer and Goodfellow et al. (1987) and Goodfellow and Geldsetzer et al. (1988: 18–20) attribute the Frasnian / Famennian mass extinction to an anoxic event caused by a meteorite impact. Reasons against a meteorite impact are discussed above in item (a).

Finally, some authors have proposed models for the Kellwasser Event, which deal with increased precipitation or the evolution of land plants. These models are discussed in detail and rejected by May (1996: 339). Therefore, it can be stated that all previous models are not able to explain the causes of the Devonian bioevents without contradictions. The best explanations are given by the models subsumed under (e) anoxic events, but these models fail to explain why anoxic events occur.

4.3. New model for the explanation of the Kellwasser and other bioevents

In the following I want to develop a new model (Fig. 2) for the explanation of the Devonian bioevents. Essentially, this new model is a further development of the **oceanic anoxic event** model of Schlanger and Jenkyns (1976: 181–182). This new model better substantiates the processes of how the **oceanic anoxic event** developed, and shows the connections to the bioevents.

In the deeper parts of the **recent** oceans, the water is cold and oxygen-rich, because in the ice-covered polar regions cold oxygen-rich surface water sinks owing to higher density, and forms the global deep sea water. This mechanism works only, if the temperature of the polar surface water is below 5°C (Wilde and Berry 1984: 144–145; 1986: 82). Within the Devonian the situation was totally different, because the poles then had no ice caps and the climate was warm world-wide.

In Devonian times, the densest surface water was produced at the salinity maximum in mid-latitudes (Wilde and Berry 1986: 82). This warm – and consequently oxygen-poor – salty surface water formed the deep water world-wide, so that the deeper parts of the oceans were permanently deficient in oxygen. Consequently, dysaerobic or anaerobic conditions were the normal situation in the deeper parts of the Devonian oceans, whereas the shelf seas were sufficiently oxygenated (Fig. 2A). The nutrient content of the shelf seas was also very low [superoligotrophic conditions of Martin (1995: 7)].

The situation in the Devonian ocean becomes problematic during times of a fast and strong sea-level rise. Such fast strong rises are documented by the sea-level curves of Johnson et al. (1985) and Johnson and Sandberg (1988) several times. A fast strong sea-level rise results in a corresponding fast and strong transgression, which has following consequences:

(1) On the one hand, this transgression leads to a considerably increased influx of nutrients stemming from increased erosion. On the other hand, shallow marine areas are greatly enlarged, which are largest production areas of organic matter. Both processes result in an increased primary production of organic matter (especially in a phytoplankton acme) and reinforce one another.

(2) Simultaneously the transgression enlarges the global ocean surface and reduces the global land surface. The very largest part of the Devonian land was without vegetation. The surface of such a desert reflects 30 – 35 % of the sun radiation, but the ocean surface reflects only 3 – 6 % of the sun radiation (e.g. Barron et al. 1980: 29; Andel 1994: 58). Therefore a transgression causes a decrease of the global albedo and consequently results in a global warming of the climate and the oceans. With increasing temperature, the gas solubility of the ocean water decreases and, automatically, the oxygen-supply of the oceans gets worse.

(3) The simultaneous working of these processes – items (1) and (2) – causes a fast rise of the upper boundary of dysaerobic (up to anaerobic) conditions in the water column, so that in large parts of the shelf sea the water near the bottom is oxygen-poor, which results in the sedimentation of black shales and black limestones. In other words, an **oceanic anoxic event** occurs (Fig. 2B).

(4) During the **oceanic anoxic event**, the largest part of the shallow marine benthic fauna is dependent on the drastically reduced areas with a good oxygen-supply at the sea bottom. These areas are only a narrow belt between the littoral zone and the area of dysaerobic or anaerobic water. Extinction is caused by the stress factors of the necessity of migration, area decrease, and isolation of populations, which result from this situation. Also, the problems which are caused by the differences in ability and speed of migration between the different elements of the fauna should not be underestimated. The transgression can bring previously separated biocoenoses into contact. It may be possible that several of the less abundant, stenotopic 'keystone' taxa die out, which causes the whole community structure to crash. The result is a mass extinction (Boucot 1990a: 20).

The restoration of normal conditions after the **oceanic anoxic event** can be explained in following way: Because of the wide distribution of anaerobic conditions during the oceanic anoxic event a large part of the organic matter pouring down from the uppermost water layers can no longer become decomposed, but is fixed in the sediment. Consequently the uppermost water layers become depleted in nutrients, which are necessary for the growth of phytoplankton, resulting in a reduced growth. On the other hand, a slowing down or even a standstill of the transgression reduces the nutrient supply, resulting in a reduction of the phytoplankton growth. Therefore both processes inevitably lead to a decrease of the phytoplankton growth, if the phase of fast transgression is finished. Then, the decrease of phytoplankton growth allows the sinking of the upper boundary of dysaerobic (or anaerobic) water, restoring normal conditions.

Concluding, it can be stated that an oceanic anoxic event – documented by the appearance of wide-spread black shales or their equivalents – can only occur in a phase of fast, strong transgression. If the transgression is too slow, an event will not happen. Furthermore an oceanic anoxic event is of relatively short duration, because it will disappear soon after the rate of transgression decreases.

Possibly, the above described processes of construction and destruction of an oceanic anoxic event will be reinforced by the changing carbon dioxide content of the air. These reinforcing processes should have only subordinate importance, since they are weakened by opposed processes.

Within the construction phase, the temperature increase caused by the transgression leads to an increased degassing of carbon dioxide from the oceans, resulting in an increasing carbon dioxide concentration of the air. This increases the natural greenhouse effect and reinforces the global warming. In opposition to this process is the fact that the increased primary production of organic matter withdraws more carbon dioxide from the ocean and atmosphere.

During the phase of restoration of normal conditions after the oceanic anoxic event, the fixation of organic matter in the sediment causes a slight decrease of the carbon dioxide concentration of the air, resulting in a decreasing greenhouse effect and decreasing global temperatures. This increases the gas solubility and improves the oxygen-supply of the ocean a somewhat. This recovery process is likely to have only minor importance because of its limitation by a negative feedback. The improvement of the oxygen-supply of the ocean causes an increased oxidation of organic matter, by which the carbon dioxide concentration of the air increases again.

4.4. Discussion of the new model for the explanation of the Devonian bioevents

Checking the crucial criteria enumerated in section 4.1., it can be stated that the new model of oceanic anoxic events explains fully the items (1) to (3). Item (5) – no glaciation – is a necessary requirement. Likewise item (4) is explained very well. Such an oceanic anoxic event will affect mainly the shallow marine benthic fauna. The decreasing oxygen-content of the water was less of a problem for the marine flora. The living space of the plankton and the nekton was less reduced. The marginal marine to terrestrial environments were not directly affected. The deep marine benthos (e.g. corals of the basinal facies) already was adapted at an oxygen-poor environment, so that it should have little problem with the upward rising and expanding of this environment. The step-wise (e.g. not abrupt) extinction can be explained following (Boucot 1990a: 20). At first the less abundant, stenotopic taxa died out, to the point where the keystone taxa were eliminated. This results in a collapse of the whole community. A further possible explanation is that the oceanic anoxic event did not occur suddenly, but had to be built up during a certain interval of time.

The new model also explains some remarkable isotope anomalies reported from the lower Kellwasser-Limestone and from the upper Kellwasser-Limestone of several localities in different parts of Europe as well as from Morocco, Nevada, and Australia. In these areas, a sudden, considerable increase of the δ^{13}C ratio has been documented (e.g. McGhee and Orth et al. 1986: 778–779; Buggisch 1991: 60–63, Fig. 7–9; Halas et al. 1992; Joachimski and Buggisch 1993; Joachimski and Buggisch 1994: 87). This increase of the (δ^{13}C ratio in the sediments of the anoxic event must be interpreted as a result of a strong acme of the phytoplankton. This fits very well with the phytoplankton-growth required for the model of oceanic anoxic events. An equivalent δ^{13}C increase was observed within the Kačák Event by Hladíková et al. (1994).

The new model explains well the occurrence of 'Lazarus taxa', which are observed only during bioevents and are not known from times between them. An example is the alveolitid tabulate coral *Scoliopora tetralobata* Hladil and Beroušek 1991, known only from the sediments of the Kačák Event and the Kellwasser Event (Hladil 1994: 6, Fig. 1; cf. Hladil and Krejčí et al. 1991: 70–73). Because the alveolitids – and especially the genus *Scoliopora* – were more tolerant in their ecological requirements than other tabulate corals (May 1994: 148–150), they should be adapted to relatively oxygen-poor water. Probably several other new settlers after the Kellwasser Event in Moravia, which are mentioned by Hladil and Krejčí et al. (1991: 58) and Hladil and Kalvoda (1993: 22), were adapted to relatively oxygen-poor water, too. Similar Lazarus taxa are reported by Becker (1993a: 137, 140, 150–152) from the lower Kellwasser Event, the upper Kellwasser Event, and comparable bioevents of the Famennian. During and / or directly after the spreading of dysaerobic (or anaerobic) water happened, an expansion of primitive ammonoid faunas, which are not known from sediments built under normal conditions took place. These ammonoids were probably adapted to relatively oxygen-poor water. Furthermore, the increased frequency of *Hyalospongea* from the uppermost Frasnian on, mentioned by McGhee (1982: 496), must not be interpreted as a proof of climate cooling (cf. Stanley 1987: 83), but is evidence for relatively oxygen-poor water.

In this context it is important that Lethiers and Casier (1995) could prove that during the upper Kellwasser Event the oxygen-content of the water near the bottom was low (about 1–1.5 ml / l O_2) as indicated by ostracod faunas.

5. Explanation of the difference of intensity of the Devonian bioevents

After answering the first question given in chapter 1, the second question remains: Why was the effect of the Devonian bioevents prior to the Kellwasser Event considerably smaller than the effect of the Kellwasser Event?

Surely, one reason for the magnitude of the extinction event in the uppermost Frasnian is the fact that **two** successive oceanic anoxic events comprise the Kellwasser Event. The ecosystem had insufficient time to recover between events. Consequently, the main extinction is in the upper Kellwasser Event (Schindler 1990: 83–84). However, close succession of two events is not an exhaustive explanation for the disastrous effect of the Kellwasser Event.

A remarkable increase of the intensity of the bioevents is visible from the Daleje Event to the Kellwasser Event. The Daleje Event and the Choteč Event each affected the fauna only slightly, whereas the Kačák Event and the Taghanic Event each eliminated a considerable number of taxa, and the Kellwasser Event devastated the shallow marine fauna. The intensity of the bioevents shows a strong negative correlation with the level of provincialism. In the Emsian, at the highest level of provincialism, the lowest intensity of extinction is observed, but in the Frasnian, at the lowest level of provincialism, the greatest extinction is observed. This correlation can be explained in following way:

(1) If, during a time of high provincialism, an ecosystem collapses, there exists may be in the vicinity of such an ecosystem many other, more or less independent

ecosystems, which may be affected only slightly or not at all by the triggering event. From these (geographically and/or ecologically) neighbouring ecosystems the space of the collapsed ecosystem can be re-settled rapidly. Besides, it is possible that these neighbouring ecosystems were refugia (cf. e.g.: Hladil 1994) for some taxa of the collapsing ecosystem. In a time of low provincialism, there are not so many neighbouring ecosystems, so that a flight in refugia or a re-settlement will be much more difficult.

(2) A high level of provincialism documents that there was only a relatively small exchange of fauna and water between the different oceans (or parts of one ocean) to different degrees. Under such conditions it is quite possible that the same oceanic anoxic event is developed in different oceans (or parts of an ocean). This would make a flight in refugia or a re-settlement easier for the fauna.

Remembering that in the Frasnian the shallow marine benthos was ±uniform world-wide, it is justified to interpret the known shallow marine areas of the Frasnian as a uniform ecosystem with a tropical character. In such a world-wide ±uniform ecosystem, an oceanic anoxic event must have a much larger effect as a comparable event in a more provincial world. At the time of the collapse of the Frasnian shallow marine tropical ecosystem, only a very few (geographically and/or ecologically) neighbouring ecosystems existed. From these, only a few sources of re-settlement were possible, and the tropical fauna had only very few opportunities for a flight in possible refugia. These considerations show that the very low diversity of the Famennian shallow marine benthos and the long time, which was necessary for the rebuilding of the complex ecosystem reef, are the very probable consequences of the conditions before the Kellwasser Event. These conditions before the Kellwasser Event – the cosmopolitanism and the uniform tropical climate – can be derived directly from the global rise in sea-level (see chapters 2. and 4.3.).

After the Kellwasser Event, further bioevents occurred within the Famennian, which are connected with eustatic sea-level rises and are probably caused by oceanic anoxic events. A compilation is given by Becker (1993a). The bioevents of the Famennian are mainly documented in the ammonoid evolution (e.g. House 1985; Becker 1993a). Because of the low diversity of the shallow marine benthos, which resulted from the Kellwasser Event, the effects of later Famennian bioevents are not so clearly visible in the shallow marine benthos.

6. Conclusions and open questions

In chapter 2 it is stated that within the Devonian the development of the provincialism of marine fauna was the result of the development of the global sea-level. Within the Emsian the sea-level was low and the level of provincialism of marine fauna was high, within the Frasnian the sea-level was high and the level of provincialism of marine fauna was low. Especially during some transgressive intervals, which also produced bioevents (chapter 3), the degree of provincialism was rapidly reduced.

Chapter 4 explained that the best model for the most of Devonian bioevents is the occurrence of oceanic anoxic events. In this model, the oceanic anoxic event is the result of a rapid transgression, which is caused by a rapid sea-level rise. The fact that the intensity of the bioevents increased from the Emsian to the Frasnian, is explained by the decrease of the level of provincialism of the marine fauna during this time (chapter 5).

Both the development of provincialism and the occurrence and intensity of bioevents within the Devonian can be deduced directly or indirectly from the development of global sea-level. This comprehensive attempt of explanation has the advantage of needing only a very few influencing factors and totally negates incalculable influences (e.g. meteorite impacts). Nevertheless, some important questions need further treatment:

(1) Are calculations able to confirm the new model for the explanation of the Devonian bioevents?

The new model of oceanic anoxic events, presented in the chapter 4.3., deals with parameters like the changing of the land area, the resulting temperature increase, etc. Generally, it should be possible to prove by estimations and calculations with mathematical models, if the expected effects are large enough to produce oceanic anoxic events.

(2) What is the cause of the sea-level changings?

My considerations are based on the sea-level curves of Johnson et al. (1985) and Johnson and Sandberg (1988), which are confirmed by many observations and investigations. Nevertheless, the cause of the sea-level changings is not known, which is a general problem in earth history (cf. Andel 1994). It is only clear that the sea-level changes are **not** glacially caused, because there are no traces of a glaciation during the Emsian to Lower Famennian. Probably the model proposed by Johnson et al. (1985: 585) is the best explanation available.

(3) Is the new model for the explanation of bioevents, that is oceanic anoxic events, transferable?

The presented model has been developed for the bioevents of the Emsian to Frasnian, but, generally, it should be transferable to other oceanic anoxic events and bioevents. But there are two restrictions: (1) This model works only in times without a polar ice cap. (2) It is not fully clear, if and how the processes are modified by the evolution of terrestrial vegetation (cf. May 1996: 345). Nevertheless, the presented model may be a good explanation for many bioevents in different times. The following two examples are suggestive:

Surely, the presented explanation of bioevents by oceanic anoxic events is also valid for the bioevents of the Famennian distinguished by House (1985: 20), Kalvoda (1986) and Becker (1993a). The *annulata* Event is an especially typical example that can be explained by the presented model of oceanic anoxic event, because it shows eutrophisation and widespread black shales, which are connected with a rapid transgression (Becker 1992: 16–17; Becker 1993a: 144–145, 150).

Another probable example is the Cenomanian / Turonian Event. For the anoxic sediments of this time – without polar ice – the oceanic anoxic event model was developed by Schlanger and Jenkyns (1976). The Cenomanian / Turonian Event is connected with a transgression and with a mass extinction (Kauffman 1986; Harries and Kauffman 1990). In the sediments at the Cenomanian / Turonian boundary very increased $\delta^{13}C$ ratios are observed (Jenkyns 1985: 510–512; Hilbrecht et al. 1986; Peryt and Wyrwicka 1993).

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