Cascade of causally linked effects of rapid glaciation-deglaciation events: a possible cause of non-selectivity of mass extinctions

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ABSTRACT. Absence of selectivity during mass extinctions in marine realm is regarded as a artificid feature appearing when a mass extinction is examined as a singular event without any inner structure. Cascade of causally linked effects of rapid glaciation-deglaciation event, as a model of mass extinction killing mechanism, may explain both the stepwise pattern of mass extinctions and the broad ecological spectrum of their victims. The coupling of glaciation and rapid deglaciation can lead to a decline of thermophilous organisms during the glaciation period and disappearance of many stenohaline pelagic and benthic aerobic organisms during environmental perturbances at the time of rapid deglaciation. They further broaden the ecological spectrum of the organisms wiped out. Mechanisms of rapid glaciation and deglaciation are discussed in detail. Abrupt onset and termination of volcanic production of sulphate aerosols are considered as one of the possible ultimate causations of the cascade of environmental changes.

KEYWORDS: mass extinction, selectivity of mass extinctions, deglaciation

1. Introduction

Characteristics discriminating mass extinctions from the background ones are, in sense of common definitions (e.g. Kauffman 1984, 1988, Sepkoski 1986), both quantitative (extinction of more than 50% of species) and qualitative (genetically and ecologically diverse species or several phylogenetically unrelated higher taxa or clades should be wiped out). Global extent and, especially, short-term duration (1 – 3.5 Ma, cf. Kauffman 1988) of mass extinctions are other important criteria.

The qualitative criteria put emphasise on broad ecological spectrum of extinct organisms in terms of their tolerances, life strategies and combination of adaptations to various habitats. This attribute of mass extinctions was discussed in many papers as a possible non-selectivity of mass extinctions – see, e.g., the case study by Jablonski (1986a) on the end-Cretaceous history of Mesozoic molluscs. Typically for the 1980s, the non-selectivity hypothesis was consistent with renaissance of catastrophic concepts, especially with the impact hypothesis. At that time Gould (1984) concluded that "mass extinction is probably blind to the exquisite adaptations evolved for previous environments of normal times". The same conclusion was inferred by Jablonski and Raup (1995) based on the new analysis of marine pelecypod extinctions during the end-Cretaceous crisis: "some biotic factors that enhance survivorship during times of lesser extinction intensities are ineffectual during mass extinctions". The only recognised biological characteristic, which contributes to the probability of survival during mass extinction events, emerges at the level of genera or higher taxa: when geographically widespread distribution is involved.

Alternatively, some other authors argue that there is no sharp boundary between background and mass extinctions considering their selectivity (Erwin 1989, Boyajian 1991, Raup 1991, McKinney 1995). Kitchell (1990) even requires some selectivity as difference to the background extinction: "A biotic crisis labelled a mass extinction should be supported by evidence of differential survival to a series of closely related causes whereas there is no such restriction on background extinction."

Advocates of terrestrial and / or climatic causation of mass extinctions published many papers (Stanley 1984, 1987, Hallam 1987, and many others) in reaction to the excessive and universal use of the impact theory in early 1980s. Ecological tolerances supposed for some taxa that became extinct during ME (mass extinction) event are in a good agreement with the hypothesis of climatic deterioration as a causation (even though to establish a clear causal link between changes in the physical environment and global species extinctions may often be problematic). In each ME event, however, also some eurythermic taxa disappeared. Destruction of trophic webs and of other biotic interrelationships may be invoked to explain this phenomenon, at least in part. Alternatively, a climatic deterioration may be only a link in the complex chain of environmental disturbances, e.g., a part of the cascade of causally tied phenomena, triggered by some principle event which is an ultimate cause of ME. Varied mosaic of ecological groups of organisms affected during the mass extinction event would then be a result of such a "domino effect".

In this paper the sequence of different palaeoenvironmental changes, triggered by a rapid glaciation-deglaciation event, is discussed as a candidate to explain mass extinction non-selectivity and magnitude.

2. Non-selectivity of mass extinctions as an emergent feature

Survival chance is not a simple feature; it has several components: (1) adaptive features such as physiologic tolerances to changes of physical and chemical parameters of environment, living strategies diminishing exposition to harmful agents, production of resting spores, seeds, etc.; (2) emergent features such as geographical range and species richness of supraspecific taxonomic categories; (3) hypothetical intrinsic ability called "evolutionary plasticity". The concept of non-selectivity of mass extinctions concerns first two aspects of extinction tolerances.

Non-selectivity of MEs appears when mass extinctions are analysed in their total, as a singular, structureless event. It is mainly a result of low-resolution of the geological record in regard of the duration of ontogenies. No ME episode has been proved to be just an instantaneous catastrophe (Boucot 1990); all of them had some duration. During Late Ordovician, Late Devonian, Late Permian and end-Cretaceous events, the data show elevated extinction measure spanning two or three chronostratigraphic stages (Benton 1995). Hypothesis of non-selectivity of MEs was based especially on statistical analysis of stratigraphic distribution of genera that used coarse time-scale (stratigraphic stages).

The fossil record may often be equivocal with respect to discrimination between gradual and simultaneous extinctions, as the distribution of the last stratigraphical occurences of a group of fossils can appear gradual due to incomplete fossil record (the Signor-Lipps effect) even if all the species became extinct simultaneously (Signor and Lipps 1982, Marshall 1995). Gradual extinction will also appear gradual in the fossil record. Thus, the hypothesis of sudden extinction cannot be rejected. In spite of this methodological problem, the fossil record of mass extinctions was considered by many authors to show generaly stepwise or gradual pattern in the scope of thousands of years (Kauffman 1986, 1988, Canudo, Keller and Molina 1986, Hallam 1987, 1988, Schindler 1990, Buggisch 1991, Keller 1993, MacLeod and Keller 1994, Longoria and Gamper 1995). As a plausible cause of the stepwise extinctions, Crowley and North (1991) consider climate instability near "critical points" in the climate systems which may disperse unstable behaviour over longer (but still geologically brief) interval of time. Theoretically, the stepness of extinctions may reflect episodic increase in strength of an ecological stressing factor, or succession of principally different stressing ecological factors which affect groups with different adaptations and habitats (these two possible mechanisms are metaphorically illustrated in Fig. 1). A stepwise extinction induced by decrease in temperature related, e.g., to a punctuated volcanic activity (cf. Cox 1988), may serve as a model example of the former type. The stepped differential stress discriminate organisms with respect to their temperature tolerances.

The non-selectivity of the ME events reported by some authors (see above) may reflect rather a number of small-scale extinction steps with different proximate causations, than a universal ecological stress which wipes out instantaneously a plenty of organisms across a broad spectrum of life strategies and ecological adaptations. Instead of one global universal proximate "killing factor", a sequence of variable environmental disturbances occurring within a geologically brief interval should be considered.

An idea that "mass extinctions are not the biotic consequences of any single phenomenon of one or another sort, but rather rare incidences of more than one major change in the physical environment accidentally clumped together within relatively short intervals of geological time, say, 2 – 4 million years in duration" is suggested by Hoffman (1989), even though, as he adds, it is not to say that all mass extinctions must be only the cluster of separate extinction episodes. He discusses the probability of coincidence of several different kinds of events which may cause large-scale extinction. High probability that at least one coincidence in a 4-million-year interval occurrs within 100 millions years is demonstrated. Erwin (1993) also considers fatal combination of deleterious environmental changes for the end-Permian massacre. Gretener (1984) illustrated the same idea by "8-dice game". From various factors, random coincidence of which could produce faunal break, he listed volcanic explosion, low temperature, reorientation of ocean currents, supernova, magnetic window, solar flare, low sea level and meteorite impact. McLaren (1983) divided these factors into proximate, immediately resulting in extinction, and ultimate, which induce cascade of causally linked proximate factors. In the natural world, as mentioned by Berry, Wilde and Quinby-Hunt (1989), multiple causes and synchroneity of events, rather than a single cause and effect, are likely to occur. Each bio-event can be connected to a hierarchy of potential causes. Each of the causes than can affect different ecological group or phylogenetic clades.

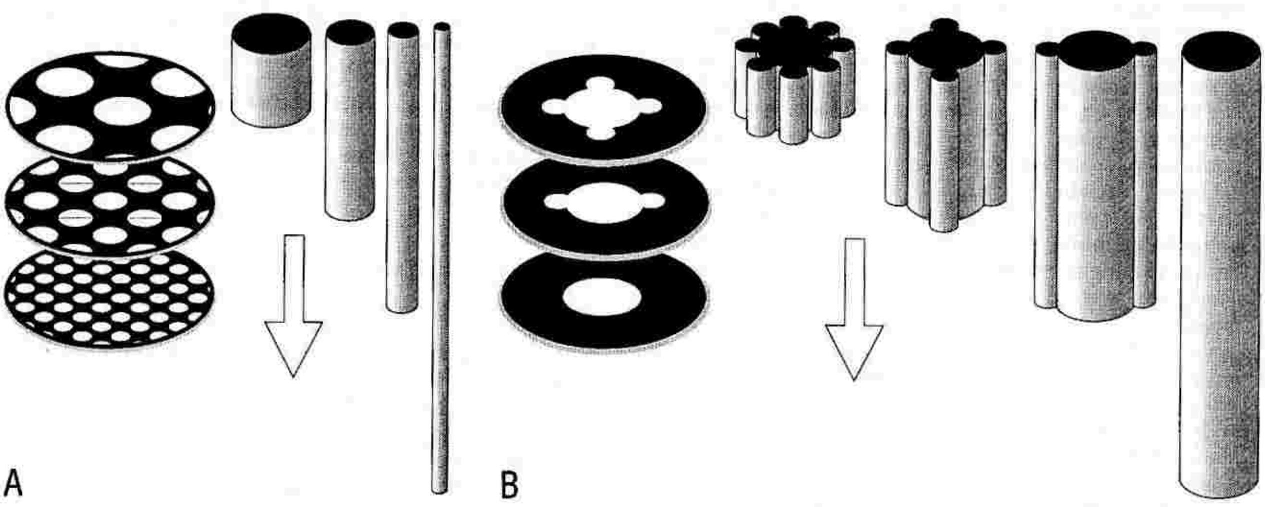

Figure 1. Two sets of sieves illustrating different models of the stepwise extinction causations. A – set of sieves with the same shape of the network openings which differ in diameter. Illustration of stepwise increase in magnitude of one selecting factor (e.g. temperature decrease). Organisms are selected with respect to single ecological factor tolerances. B – set of sieves with different shapes of openings illustrating a cascade of different selecting factors. In each step very distinct adaptational zones may be affected.

3. Mass extinction pattern

Mass extinction events occurred across a wide spectrum of environments. In our study we will concentrate on marine habitats only.

We are still unable to know the full sequence of events leading to the extinctions of individual species. Detailed studies published during last fifteen years show, however, that some general pattern in ecological adaptations and habitats of extinct marine taxa can be recognised under the mass extinction events. Kauffman (1988) recognised following phenomena common to some ME events (Cenomanian / Turonian, Cretaceous / Tertiary, and Eocene / Oligocene): all are stepwise extinctions, steps are abrupt (ca 100 ka or less), stenotopic and thermophilous species became extinct earlier.

The pattern of mass extinctions may look more or less as follows:

(a) the groups with low tolerances to cooling are affected first:
   - reef ecosystems
   - thermophilous benthic species of non-reef ecosystems
   - thermophilous pelagic species;

(b) other groups are affected later on:
   - pelagic species and organisms with planktotrophic larvae of high latitudes
   - offshore benthic organisms.

Of course, perturbances of biotic interrelationships, which cause many partial extinctions during ME events, somewhat hide the extinction pattern related primarily to disturbances in physical environment. Nevertheless, the suggested pattern implies a non-randomness in sequences of palaeoenvironmental changes. Each step of the mass extinction may be understood as a single-factor small-scale extinction and the mass extinction event as a whole as a hierarchically structured cascade of these small-scale extinctions which, in principle, do not differ from background extinctions.

4. Rapid glaciation-deglaciation model of mass extinction causation

Important feature of mass extinctions is their coincidence with major regressions (Hallam 1984, 1987, 1990, Jablonski 1986b, Wiedmann 1986, Dickins 1990), and with anoxic events (Newell 1984).

Different models were proposed, explaining mass extinctions as net result of multiple, related causes. Leary and Rampino (1990) suggested, for example, some common thread of cause and effect among large-body impacts, ocean anoxic events, and flood-basalt volcanism. In our opinion, the mass extinction mechanism, which can best explain both the broad ecological spectrum of affected species, sea level fluctuations and anoxic events, might be coupled rapid glaciation and deglaciation, especially when the cooling is caused by extraordinary volcanic activity. This mechanism can explain causal link among very different proximate causes of extinctions such as anoxic event, surface salinity change and cooling. With some modifications, it may be almost universal mechanism. Many extinctions of lower magnitude than the "Big Five" mass extinctions (e.g., the Kačák event in Devonian, Cenomanian / Turonian boundary and Eocene / Oligocene boundary – to mention some for once) might have similar causation.

4.1. The two-step glaciation-deglaciation model

Our two-step glaciation-deglaciation model integrates several "partial" scenarios of ME discussed in details by other authors. The proximate causes of discrete steps of ME processes are integrated into two cascades (or webs) of causally linked causes of ME. The first cascade is triggered by cooling and leads to environmental changes connected to glaciation. The second cascade begins by rapid warming and deglaciation. As a frequent ultimate cause of such devastating climatic fluctuation, an abrupt onset of volcanic activity producing high volumes of sulphate aerosols is considered, which can be responsible of rapid and abrupt cooling associated with development of glaciation. The end of sulphate aerosols production can be really instantaneous and induce rapid retreat of glaciation. As Renne et al. (1995) notice for the end-Permian crisis "a short-lived volcanic winter, followed within several hundred thousand years by greenhouse conditions, would fully explain the environmental extremes that caused the P-T mass extinctions".

The feedbacks in oceans during the climatic changes which induce cascade of environmental disturbances were described by Berger (1982). Important steps of the cascades are shown in Fig. 2.

The proposed two-step glaciation-deglaciation model is as follows:

(a) cascade of causally linked palaeoenvironmental events triggered by glaciation:

- sea-level fall, partial regression from shelves, retreat of seas from the epicontinental basins, (larger area of land and ice-caps increase albedo: cooling – supporting feedback, cf. Berger 1982);
- increased temperature gradient between the low and high latitudes drives the oceanic currents; high production of cold dense water in high latitudes which sinks to ocean abyss induces vigorous meridional thermohaline circulation. Although an increased transport of warm water to high latitudes restricts cooling, it induces higher evaporation in high latitudes (Lehman, Wright and Stocker 1993) which may significantly increase snow precipitations in polar areas and hence facilitate high rates of the ice-caps growth);
- more nutrients is brought to pelagial, productivity in the offshore oceans increases;
- oceans are well oxygenated near bottom due to vigorous circulation.

(b) cascade of causally linked palaeoenvironmental events triggered by deglaciation:

- melting of glaciers produces a sea-level rise;
- transgression reduces the land area, albedo decreases, global warming is accelerated;
- melting of glaciers causes decrease in the surface salinity;
- decrease in latitudinal temperature gradient and decrease in surface water density due to high fluxes of the melt water induce sluggish oceanic thermohaline circulation or its almost complete switch off;
- sluggish circulation together with high density stratification leads to decrease in the bottom oxygenation, oceanic anoxic events may develop;
- when the thermic structure is reorganised, process of oceanic turnover brings anoxic waters rich in CO_2, and sometimes possibly also toxic (H_2S) waters from the main pycnocline (100 – 1000 m) to the photic zone in pelagial and on shelves (Wilde and Berry 1984, Wilde, Quinby-Hunt and Berry 1990, A.Knoll, R. Bambach and J.Grotzinger –quotation after Kerr 1995);
- decreased input of nutrients to the oceanic photic zone restricts productivity. An ocean with strongly reduced life (something similar to the "Strangelove ocean" of Hsü 1982) may originate in response to the low fertility, decreased surface salinity and periodic turnovers bringing anoxic water to the euphotic zone.
- low oceanic production of biogenic carbonates enables growth in atmospheric CO_2 concentrations which further accelerates the global warming.

Some of the individual steps of these cascades are discussed at lengths latter.

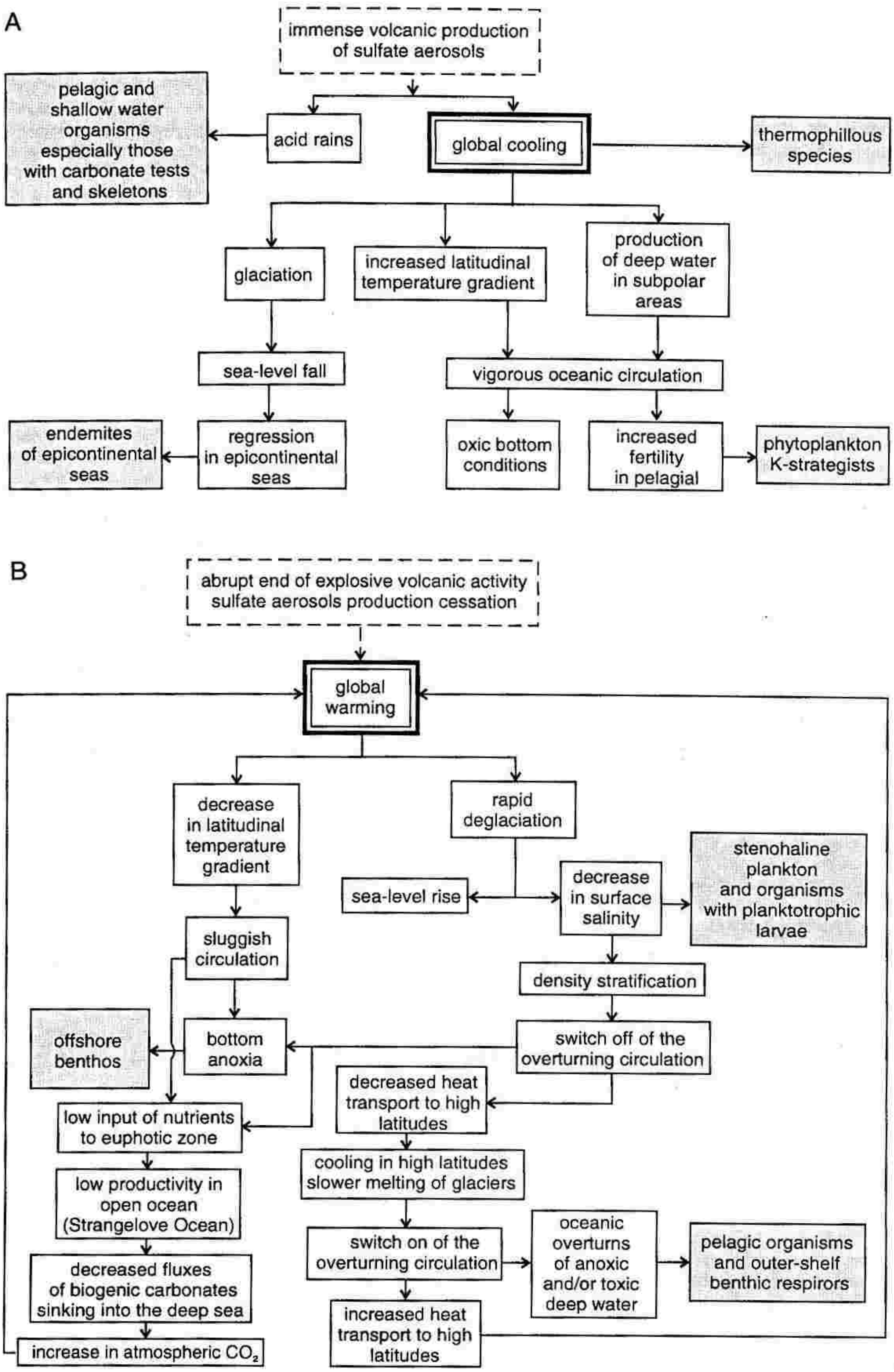

Figure 2. Cascade of environmental changes triggered by global cooling (A), and by warming after glaciation (B). Ecological groups of organisms which can be affected by the environmental changes are shown in shaded boxes.

4.2. Effects of causally linked steps of environmental changes during a rapid glaciation-deglaciation event on the biota.

Possible effects of cascade of environmental changes triggered by rapid glaciation-deglaciation event on the biota are shown in Fig. 2, for the cascade of effects caused by global cooling resulting in glaciation, and the temperature increase leading to rapid deglaciation, separately. Note that not every step of the cascade mentioned in the previous paragraph must be a proximate cause of an extinction. The impact of environmentally caused extinctions on biological structure of ecosystems, which should further broaden the ecological spectrum of affected organisms, is not shown.

4.3. Can rapid deglaciation lead to the surface salinity decrease intolerable to many pelagic species?

While effect and possible mechanisms of the oceanic anoxic events were discussed in many papers, the hypothesis of reduced ocean salinity as the cause of ME has attracted only a little attention (Beurlen 1956, Fischer 1963, Stevens 1977, Thierstein and Berger 1978, Gartner and Keany 1978, Berger and Thierstein 1979).

Fairly detailed Quaternary record gives us some possible average rates of deglaciations. Sea-level rise by ca 120 m during last deglaciation period (14,000 to 7,000 years B.P.) released 42×10^6 km^3 of water, a maximum discharge rate was of order 0.5×10^6 m^3 s^{-1} (Fairbanks 1989). If all the heat transported from low to high latitudes by conveyor circulation in modern Atlantic was taken up in melting ice, it would yield according to Lehman, Wright and Stocker (1993) 60,000 km^3 of meltwater per year, it is 1.9×10^6 m^3 s^{-1}. In reality, a part of this heat radiates to the space. It is compensated by a consumption of sunlight energy and heat transported by atmosphere. Modelling of oceanic circulation under increased glacial meltwater influx shows that overturn of circulation may be eliminated by changes in density of the surface water (more details below), and that the surface salinity may decrease in large areas of North Atlantic below 32‰ during 1000 years (Wright and Stocker 1993). It seems quite reasonable to assume that very rapid warming after the end of immense volcanic activity may bring about even more rapid melting. Another effective mechanism for a short-time deadly decrease in surface water salinity may be a catastrophic large-scale release of meltwater through megafloods from glacial and proglacial reservoirs like those supposed for the last Quaternary deglaciation by Blanchon and Shaw (1995). If resulting decrease in salinity of the surface waters drops below 28–30 ‰ in the upper 100–150 m thick layer of the water column, stenohaline plankton and plaktotrophic larvae of benthic organisms living in pelagial for a long time, will be killed, or, at least, unable of a reproduction. Vertical mixing, low in the time of sluggish circulation (lateral circulation driven by winds help to distribution of melt water over the ocean), and the rate of deglaciation, will control the salinity decrease. The latter is more important in this case than total volume of continental ice caps.

4.4. Which mechanisms can support rapid glaciation and deglaciation?

Many mechanisms can be considered a cause of rapid glaciation and deglaciation. Paleogeography and orography inhibiting latitudinal heat distribution are important conditions of most glaciations. Depending on palaeogeographic position of continental blocks and oceans, the Earth history can be divided to periods of global warm climate supporting paleogeography (e.g. poles in free oceans) and cool global climate supporting paleogeography (e.g. continents around poles).

Temperature is the main factor determining the state of the climatic system. According to the ice sheet modelling (Budd and Rayner 1993), the summer temperature deviations required for large ice sheets to grow is -4°C, and to shrink is +5°C. Important accelerating mechanism for the ice sheet formation and its melting is a high seasonality driven by orbital cycles, as the deglaciation can be supported by high summer temperatures, not only by year-round warmth (Crowley et al. 1986).

Most important triggers of the extraordinary temperature fluctuations may be:

(a) **sulphate aerosols produced by volcanic activity** (Officer and Drake 1985, Officer et al. 1987). Long-term production of 1000 megatons of SO_2 per year (Self and Thordarson 1995) may be an ultimate cause of ME, triggering both cooling and glaciation when it starts, and warming with rapid deglaciation after it ends. Hypothesis of a strong volcanic activity seems to be one of the most plausible alternatives due to possibility of its abrupt onset and abrupt end. It is the mechanism which can probably start glaciation even during the greenhouse periods. Abrupt end of sulphate aerosol production facilitates rapid return to the warm climate which existed before. The reappearance of warm conditions may induce rapid and complete deglaciation. The most rapid glaciation and deglaciation is most probable at the times of disturbed environmental stability within the greenhouse period. This kind of glaciation is "inherently unstable" (Brenchley et al. 1994). Impressive correlation of ME events with immense flood-basalt volcanism, particularly the estimated $2 - 3 \times 10^6$ km^3 of flood basalts of Siberia, produced at the Permian / Triassic boundary (Renne et al. 1995), and 1.5×10^6 km^3 of Dekkan flood basalts at the Cretaceous / Tertiary boundary (Rampino and Stothers 1988, Duncan and Pyle 1988), speaks for importance of this triggering mechanism.

(b) **changes in latitudinal heat transport by oceanic currents** (Broecker et al. 1990, Cessi and Young 1993, Winton 1993, Wright and Stocker 1993, Lehman, Wright and Stocker 1993). Oceans play a fundamental role in the Earth's long term climate. From this point of view, the crucial controls of the oceanic circulation are those influencing the latitudinal heat distribution (cf. fig. 3). A trigger of weakening or cessation of meridional overturning circulation, which operates as a "heat conveyor" transporting heat to polar areas, may be the meltwater from ice sheets. A massive influx of the fresh water reduces the salinity of surface water and hence also its density. The lowered density of the surface cold water protects it from sinking, and thermohaline circulation is disturbed (Broecker 1990, Broecker and Denton 1990). Broecker et al. (1990) suggests oscillations in salinity which modulate the strength of currents responsible of heat transport from low to high latitudes (self-sustained salt oscillator). When the formation of the low-salinity water cap switches off the conveyor circulation, the transport of heat drops down. Subsequent cooling of polar area slows down ice melting, and the surface salinity can increase again. Density of the surface water then grows up until the cold surface water begins to sink down again, and the heat conveyor current is switched on. Heat transported to polar area accelerates the melting and a new oscillation begins. Periodicity of oscillations was approximately about thousand years during the last Quaternary period of glaciation. Climatic changes during the period of strong melting are much quicker than intervals of ice rebuilding.

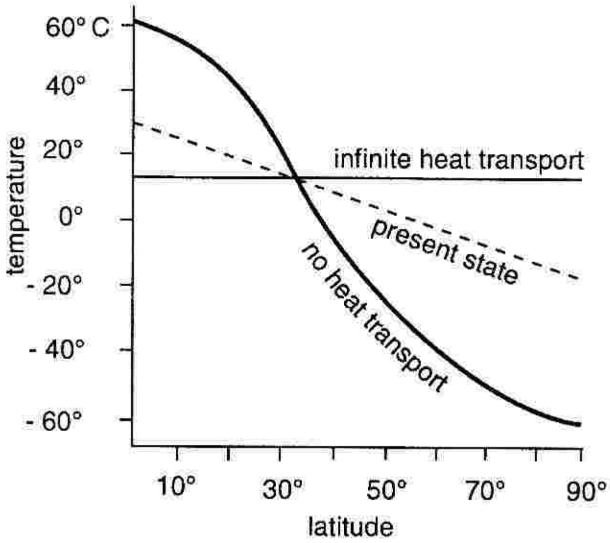

Figure 3. Graph showing influence of the heat transport on the latitudinal distribution of temperatures. Fluid transports of thermal energy between the low and high latitudes maintain the moderate temperature. Switch off of the oceanic heat conveyor may bring about increase in global temperature gradient and extraordinary warming in tropical regions, and cooling in polar ones. The circulation is driven by differences in water density determined both by temperature and salinity, and is almost independent of wind forcing. (after Crowley and North, 1991; modified).

(c) **opening and closing of oceanic gateways** (Berggren 1982). Good example is the global cooling, which began in mid-Eocene, and was connected with the Antarctic glaciation. This glaciation was enabled by openning of the straits between South America and Antarctic, and between Tasmania and Antarctic. This triggered the circum-Antarctic circulation and the isolation of Antarctica from a heat transport begun (Kennett 1977).

(d) **instability of small ice caps related to the albedo feedback mechanism** (Crowley and North 1991). The model supposes unstable state when ice cap's surface drops under a threshold limit (Fig. 4). At that time, an accelerated melting of ice sheet mağy be expected. This mechanism will accelerate the production of meltwater, especially during the complete deglaciation.

(e) **greenhouse gases produced by volcanic activity** may support warming by the greenhouse effect (Rice 1995). Warming may continue for some time after abrupt end of an immense volcanism (Renne et al. 1995), especially due to more rapid residence of the sulfate aerosols. Accelerating influence of greenhouse gasses on melting rate of ice caps may be the crucial factor, especially when the amount of transported heat to the high latitudes is low due to the switched – off conveyor circulation.

(f) **changes in CO_2 levels in atmosphere due to changes in bio-productivity** (Brenchley et al. 1994). Atmospheric CO_2 concentration can be increased by the decline of burial of biogenic carbonate in open ocean. Very low productivity of the oceanic photic zone caused by lowered imput of nutrients at the time of reduced thermohaline circulation (time of anoxic event) decreases the flux of biogenic carbonates to the oceanic bottom and may effect carbon partitioning from the atmosphere to the deep ocean (Kumar et al. 1995). This process may, however, be buffered by increased accumulation rate of organic carbon. Fluctuations in the $\delta^{13}C$ recognised around the Permian-Triassic boundary imply (A. Knoll, R. Bambach and J.Grotzinger – quotation after Kerr 1995) that carbon produced by phytoplankton could be first accumulated in deep water during the sluggish ocenic circulation phase and then, at the time of oceanic turnover, transported to the shallows and released to the atmosphere.

(g) **changes in elevation of ice sheets.** Dramatic ocean-atmosphere reorganizations may result from atmospheric threshold changes induced by a rapid increase or decrease in an ice sheet elevation (due to accumulation of ice and its melting, respectively; Blanchon and Shaw 1995). It may be especially important as accelerating mechanism at the time of deglaciaton.

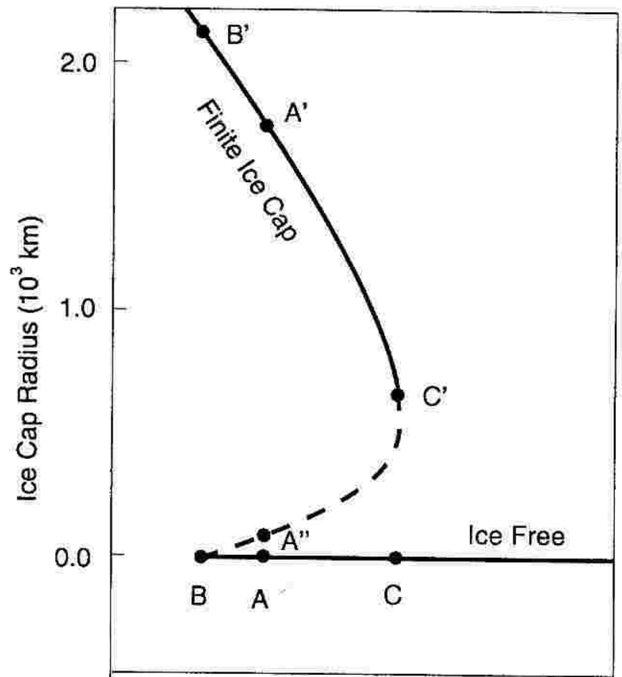

Figure 4. Schematic graph of equilibrium solution of an energy balance model with ice-albedo feedback. More than one equilibrium solution (e.g. A, A') may exist for the same external boundary conditions, intermediate solutions (e.g., A") are unstable. As boundary conditions are slowly changed, the possibility of rapid transition between climate states results. This feature has been called "the small ice cap instability". (Graph and explanation after Crowley and North, 1991).

(h) **impact of an extraterrestrial body.** Increase in temperatures perhaps by 30°C for ca 30 days during the K / T event is supposed by O'Keefe and Ahrens (1982, quotation after Crowley and North 1991). The sea-level fall and shift in oxygen isotope record some time before the origination of the Ir-anomaly layer suggests a cooling period (there is, however, still no geological evidence of a glaciation) which could be interrupted and upset by an impact event.

4.5. Does evidence of rapid glaciation and deglaciation at the time of ME events exist?

Unlike the previous views of geologists, recent evidence suggests that the ice-free periods (without polar ice caps) in geological history of the Earth were probably rare (Frakes and Francis 1988, Robin 1988, Weissert and Lini 1991). From the geological point of view, high rates of sea-level falls were recognised in geological record around the majority of ME levels. High rates of the sea-level falls point most likely to glacioeustatic driving.

The major **late Ordovician** glaciation, well evidenced in geological record, was probably confined to the Hirnantian and was only 0.5 – 1 Ma long. Oscillations in oceanic circulation, based on the carbon isotope record, were recognised. The phases with warm saline bottom water alternated with those characterised by cold deep-water circulation (Brenchley et al. 1994). Estimated magnitude of the sea-level fall was 60 m, or 45 m with isostatic adjustment (Crowley and Baum 1991). Brenchley (1990) pointed to two-step extinction during the end-Ordovician event. The first episode was evidenced at the beginning of major regression at the end of Rawtheyan (the penultimate stage of the Ashgillian), and the second one at the time of transgression near the end of Hirnantian .

The Upper Kelwasser event at the **Frasnian / Famennian boundary** lasted maximally first hundreds of thousands years, while biotic crisis interval lasted altogether 1-2 Ma (Schindler 1990, 1991). The event was connected probably to several fluctuations of the sea-level (Kalvoda 1986, Buggisch 1991). Evidence of approximately synchronous glaciation comes from South America (Caputo 1985). Palaeontological record also suggests a significant drop of global temperature during the F / F event.

Around the **end of Permian**, glacial and glaciomarine deposits are abundant in Australia, Siberia, and the Kolyma block (Maxwell 1989). A sea-level fall was recognised at the end of Tatarian (P / T boundary) and also 5 Ma before, at the end of Guadalupian. Some estimates of the sea-level fall at the P / T boundary consider up to 280 m (Holster and Magaritz 1987 – quotation after Campbell et al. 1992), others about 150 m. A temporary global shift in isotopic ratios of carbon during the final 100,000 years of the Tatarian presumably relates in some way to the severe Tatarian extinction (Stanley and Yang 1994). Time interval of the Tatarian ME event is comparable with duration of Pleistocene glacial periods. Wignall and Hallam (1992) recognised an extremely rapid transgression above a minor sequence boundary in the late Permian, leading to the development of the relatively deep-water pyritic micrite – a maximum flooding surface at the Permo-Triassic boundary. Highly probable causal link to the Siberian trap volcanism is supported by the same radiometric age and the short duration of the volcanism (less than 1 Ma, Courtillot 1995, Renne et al. 1995).

The **end-Triassic** total extinction rate of marine organisms is very high (Benton 1995). Hallam (1981) reports the regression and loss of reefal facies, succeeded by a major transgression and widespread bottom anoxicity across the Triassic-Jurassic boundary. There is, however, no isotopical evidence of temperature change for the end-Triassic crisis (Hallam and Goodfelow 1990).

There is still no record of glaciation around the **end-Cretaceous event** even though, for example, Hallam (1988) did not principally excluded the possibility. On the other hand, many observations point to a rapid sea-level fall just before the Cretaceous / Tertiary (K / T) boundary (Haq et al. 1987). Estimates of magnitude vary from 80 m (Haq et al. 1987) to 130 m (Donovan et al. 1988). Characteristic excursions of the oxygen isotopes show sudden and severe cooling followed by rapid warming at the K / T boundary (Hsü et al. 1982, Keller and Lindinger 1989, Sarkar et al. 1992). Negative shift 2.5‰ in $\delta^{18}O$ at or just above the K / T boundary (Rampino and Volk 1988) may, however, be influenced partly by a change in the oceanic water chemistry. Negative shifts in ^{18}O are typical of deglaciation period when higher input of meltwater decreases the surface salinity (decrease of $\delta^{18}O$ by 0.11‰ corresponds to 1% decrease in salinity, Craig and Gordon 1965; Quaternary glaciation is believed to have caused about 1.5‰ fluctuation in the $\delta^{18}O$, Emiliani and Shackleton 1974). Development of low-oxygenated bottom water has been recorded from the K / T boundary, too. Based on quantitative benthic foraminiferal analysis from the first metre above the K / T boundary, Keller (1988) noted decrease in bottom oxygen in depths of outer to middle shelf in El Kef section (Tunisia).

4.6. Why are not all glacial periods of geological history connected with mass extinction events?

Probably each of the causations ever considered as a cause of ME can be sometimes recognised in a stratigraphical level where no pronounced extinctions can be recognised, although the causal factor magnitude is comparable to that of ME times. In some circumstances, a cascade of proximate causes, complex and unique situation of environmental factors, and different situation with respect to previous history of ecosystems evolution can be invoked. The last explanation was used by Crowley and North (1991) against arguments that climatic change cannot be considered a cause of MEs due to low measure of extinctions during the late Pleistocene glaciation. They stated that during three Cenozoic periods of global cooling (Eocene / Oligocene transition, Mid-Miocene and Late Pliocene) many of the forms sensitive to extinctions were eliminated, so that the ecological niches for a number of groups that were very sensitive to extinctions had already been removed millions of years before the Pleistocene. It is clear that the most extensive reduction of diversity can be expected after a long time of relative environmental stability, which facilitates conditions for diversification of ecosystems .

Extinction of about 80% of marine species at the end of Permian (end of Tatarian stage), only 5 Ma after the end-Guadalupian ME event with about 71% species becoming extinct (Stanley and Young 1994), seems to be contradictory to these suggestions. Nevertheless, the magnitude of extinction cannot be considered as a function of environmental changes amplitudes only.

Another reason of the absence of correlation of glacial periods with ME events may be a very rare occurrence of rapid deglaciation capable of the ample surface salinity decrease and the triggering of subsequent cascade of environmental changes.

5. Conclusions

The non-selectivity of mass extinction events is an artificially emerging feature when proceeding them as singular, undifferentiated events.

Stepwise, or gradual character of MEs and some general pattern in succession of ecological tolerances and adaptations of the mass extinction victims suggest the non-randomness in sequences of paleoenvironmental changes. The two-step model of rapid glaciation and rapid deglaciation may explain a broad ecological spectrum of mass extinction victims by a variety of perturbances brought on by a cascade of causally linked paleoenvironmental changes. Apart from the effects of cooling and anoxia on marine biota, deadly perturbances in pelagic ecosystems may be brought about by decrease in surface water salinity due to catastrophic release of meltwater during extremly rapid collapse of ice sheets. One of the possible causes of most rapid glaciation-deglaciation events may be an immense volcanic eruptive activity like that which produced the Siberian traps at the Permian-Triassic boundary, or the Deccan traps at the Cretaceous-Tertiary boundary. However, other causes of rapid glaciation-deglaciation events (e.g. paleogeographic changes) can be ultimate causes of mass extinctions as well.

Individual glaciation-deglaciation events recognised (and maybe also those not recognised yet) through the Phanerozoic might highly differ in their course, magnitude of individual steps and pattern of palaeoenvironmental perturbations. The working model presented in the paper rather suggests the style of possible causal links and their variable impact on biota than being a rigid just so story of all mass extinctions.

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