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Splash-like marine biodiversity additions after the Cambrian

DMITRY A. RUBAN¹

Abstract. Some Phanerozoic biotic radiations in the marine realm led to marine biodiversity additions, i.e., increases in the global number of genera to unprecedented levels. Each of the two alternative biodiversity curves implies five post-Cambrian events of this kind, which coincided with parts of the biotic radiations. However, differences between these curves do not allow to find coherent marine biodiversity additions with the only exception of those occurred at the interval of the Great Ordovician Biodiversification. The attempted interpretations indicate that the marine biodiversity additions increased the number of marine genera by 10–30 % (from the previous unprecedented level to that new). All additions were relatively brief and occurred as splashes throughout the Phanerozoic. Peculiar intrinsic and extrinsic factors, as well as the speed of diversification should be considered when triggers of these events are looked for. Undoubtedly, splash-like marine biodiversity additions played an important role in the evolution of life in the sea, but a lot of research is required in order to understand their true nature.

Key words: marine biodiversity, radiation, evolution, Phanerozoic.

Апстракт. Поједине биотичке радијације које су се догодиле у морским областима током фанерозоика додатно су утицале на разноврсност морских организама (додатно морска радијација), односно утицале су на повећање бројности родова на глобалном нивоу које до тада није било познато. Свака од две алтернативне криве биодиверзитета указују на пет посткамбријумских догађаја овог типа, који се подударају са деловима биотичке радијације. Ипак, разлике између ове две криве не омогућавају да се закључи о јединственој појави повећавања морског биодиверзитета са изузетком који је присутан у периоду велике ордовицијумске биодиверсификације. Објашњење дато овом приликом указује да је додатно увећање морске разноврсности довело до повећања морских родова за 10–30 % (од предходног нивоа до новог нивоа). Сва додатна повећања разноврсности била су релативно краткотрајна и појавила су се као бљесак током фанерозоика. Посебни унутрашњи и спољашњи фактори, као и брзина диверзификације требало би да буду узети у обзир приликом разматрања узрока ових догађаја. Без сумње, муњевити додатни морски биодиверзитет игра важну улогу у еволуцији живота у мору, али неопходно су додатна истраживања како би се боље разумео његов прави карактер.

Кључне речи: морски биодиверзитет, радијација, еволуција, фанерозоик.

Introduction

Marine biodiversity neither remained stable, nor increased gradually through the Phanerozoic; it experienced significant fluctuations (SEPKOSKI *et al.* 1981; RAUP & SEPKOSKI 1982; SEPKOSKI & RAUP 1986; SEPKOSKI 1993; BENTON 1995, 2002; PETERS & FOOTE 2001; FOOTE 2003, 2007; BAMBACH *et al.* 2004; BAMBACH 2006; BENTON & EMERSON 2007; STANLEY 2007; ALROY *et al.* 2008; PURDY 2008; MILLER *et al.* 2009;

ALROY 2010; KIESSLING *et al.* 2010; LIEBERMAN & KAESLER 2010; MARSHALL 2010; BUSH & BAMBACH 2011; HANNISDAL & PETERS 2011; HEIM & PETERS 2011; MELOTT & BAMBACH 2011a,b; PETERS & HEIM 2011; ABERHAN & KIESSLING 2012; ABERHAN *et al.* 2012; VALENTINE *et al.* 2013; MANNION *et al.* 2014). There were several major radiations in the history of the marine life, including those occurred in the Cambrian and the Ordovician (SEPKOSKI & SHEEHAN 1983; DROSER & SHEEHAN 1995; DROSER *et al.* 1996;

¹ Department of Tourism, Higher School of Business, Southern Federal University, 23-ja linija Street 43, Rostov-na-Donu, 344019, Russia; address for postal communication: P.O. Box 7333, Rostov-na-Donu, 344056, Russia. E-mails: ruban-d@mail.ru, ruban-d@rambler.ru

MILLER & FOOTE 1996; GEYER 1998; CONWAY MORRIS 2000, 2003; CONNOLLY & MILLER 2001, 2002; MILLER & CONNOLLY 2001; WEBBY 2001; KIRSCHVINK & RAUB 2003; DZIK 2005; HARPER 2006; LIEBERMAN 2008; MARUYAMA & SANTOSH 2008; SERVAIS *et al.* 2008, 2009, 2010; TROTTER *et al.* 2008; BRASIER 2009; MASUDA & EZAKI 2009; MEYER 2009; VANNIER 2009; PLOTNICK *et al.* 2010; RUBAN 2010, 2013; MALETZ *et al.* 2014; SANTOSH *et al.* 2014). However, many of these radiations were only recoveries after precedent biodiversity losses. For instance, the number of genera increased strongly in the Middle Triassic, but this radiation did not permit marine invertebrates to reach the same diversity as it was before the Permian/Triassic mass extinction (ALROY *et al.* 2008; PURDY 2008). Therefore, it appears very important to focus on those time intervals, when the marine biodiversity reached unprecedented levels. Such radiations (often parts of longer radiations) can be called “biodiversity additions”. An interest to them is also facilitated by the present discussions of thresholds for the global biodiversity and carrying capacity of the planetary ecosystem (ABERHAN & KIESSLING 2012; ABERHAN *et al.* 2012; RUBAN 2013).

The issues relevant to the marine biodiversity additions were considered earlier by ALROY *et al.* (2008), ABERHAN & KIESSLING (2012), ABERHAN *et al.* (2012), and RUBAN (2013), but in only general form. The main objective of the present brief paper is to establish biodiversity additions in the post-Cambrian evolution of the global marine fauna on the basis of the already-documented Phanerozoic biodiversity changes. The Cambrian is excluded from the present analysis because much has been told already about the so-called “Cambrian explosion” (GEYER 1998; CONWAY MORRIS 2000, 2003; KIRSCHVINK & RAUB 2003; DZIK 2005; LIEBERMAN 2008; MARUYAMA & SANTOSH 2008; BRASIER 2009; VANNIER 2009; PLOTNICK *et al.* 2010; RUBAN 2010; ERWIN & VALENTINE 2013; MALETZ *et al.* 2014; SANTOSH *et al.* 2014).

Terms, original biodiversity curves, and method

Marine biodiversity addition can be defined as a long-term event in the biotic evolution, when the biodiversity increased from the previous unprecedented level to the new unprecedented level (Fig. 1). Evidently, such an event differs from “usual” biotic radiations, including those Paleozoic major radiations recognized in the marine realm by RUBAN (2010). Radiation (*sensu lato*) is an increase in the biodiversity from the minimum to the maximum. If the minimum was below the previous unprecedented biodiversity level and the maximum was above it, the only part of the radiation corresponded to the marine biodiversity addition (Fig. 1). And in those rare cases, when the biodiversity reached unprecedented level, remained

on its for some time, and then started to rise again, this latter rise marks the radiation, which completely coincides with the biodiversity addition. The definition presented above may leave an impression that each biodiversity addition is an “occasional” event. However, one should note that reaching unprecedented level of biodiversity means fundamental change in the ecological state of the planet, which begins to sustain a higher number of organisms than anywhen earlier. The proposed idea of the marine biodiversity addition is linked to the modern ideas on thresholds for biodiversity, global carrying capacity, etc. (ABERHAN & KIESSLING 2012; ABERHAN *et al.* 2012; RUBAN 2013).

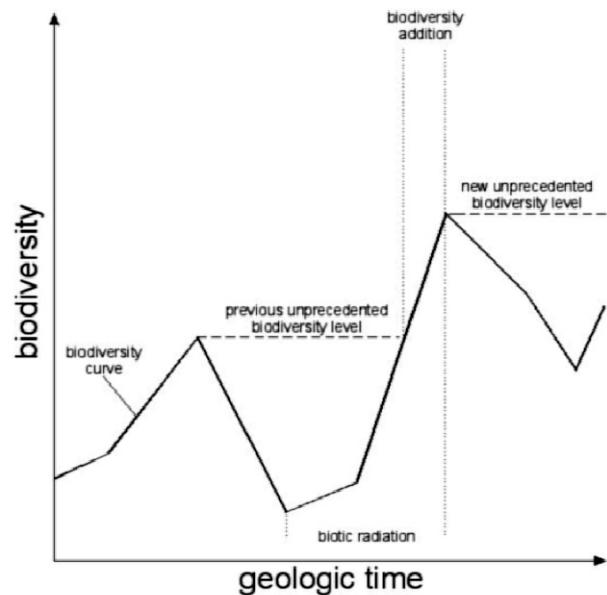


Fig. 1. A simple graph demonstrating biodiversity addition (projected on the geologic time line by dashed lines) and its relationship with biotic radiation (projected on the geologic time line by grey area).

Following its definition, the marine biodiversity additions can be identified on the basis of graphical analysis of “simple” biodiversity curves reflecting total number of taxa and their changes through the geologic time. Now, two curves are available (Fig. 2). The first curve was proposed by PURDY (2008, Fig. 1, p. 653) on the basis of the “classical” palaeontological database compiled by SEPKOSKI (2002) (this database is also available on-line: strata.geology.wisc.edu/jack/start.php). The second curve was proposed by ALROY *et al.* (2008, Fig. 1, p. 98) on the basis of the new palaeontological database (available on-line: paleodb.org). The both reflect changes in the number of genera of marine organisms (chiefly invertebrates) throughout the Phanerozoic. When the first curve is reconstructed via “simple” calculation of the number of genera per geologic time intervals, the second curve employs a more complex, sample-standardized approach (see

ALROY *et al.* (2008) for details and BENTON *et al.* (2011) for discussion of the utility of this approach). In the other words, these are alternative curves presenting different views on marine biodiversity, and the both should be considered in the analysis of marine biodiversity additions. The other reconstruction of ALROY (2008, Fig. 4, p. 100) is not considered in this article, because it does not depict really alternative curves.

Analysis of each biodiversity curve (ALROY *et al.* 2008; PURDY 2008) allows to outline radiations in the marine realm between the minima and maxima in the total number of genera. Presumably, the “Cambrian explosion” reflects the first Phanerozoic unprecedented level of biodiversity. The curves permit to find the forthcoming biodiversity increase, when this level was exceeded and, consequently, the new unprecedented level was established. This increase is the marine biodiversity addition. Projecting it on the geologic time line allows to evaluate its duration in the history of the Earth. Then, the procedure is repeated to look for the next biodiversity additions.

The present study is based on the modern relative and absolute time scales developed by the International Commission on Stratigraphy (GRADSTEIN *et al.* 2012; see on-line: www.stratigraphy.org). Differences between the time scales employed by ALROY *et al.* (2008) and PURDY (2008) and the modern chronostratigraphy

should be considered. Some modern developments in the lower Paleozoic chrono- and biostratigraphy and absolute geochronology (OGG *et al.* 2008; COCKS *et al.* 2010; LOYDELL 2012; COMPSTON & GALLAGHER 2012) are also taken into account. Formal chronostratigraphical units are capitalized (e.g., Middle Ordovician, Late Cretaceous, etc.) in this article to be distinguished from those informal, which are not capitalized (e.g., early Paleozoic, late Oligocene, etc.).

Nomenclature of post-Cambrian marine biodiversity additions

A total of five post-Cambrian marine biodiversity additions can be established with each original curve (ALROY *et al.* 2008; PURDY 2008) to be labelled A1–5 and S1–5 respectively (Fig. 2, Tables 1, 2). The curve of PURDY (2008) permits to establish the only marine biodiversity addition in the Paleozoic and a series of such events in the late Mesozoic–Cenozoic (Fig. 2, Table 1). The curve of ALROY *et al.* (2008) implies “concentration” of marine biodiversity additions in the early Paleozoic and two “separate” events in the end-Paleozoic and the end-Mesozoic (Fig. 2, Table 2). The only A2 and S1 events coincided, whereas the other interpreted additions did not. The noted coinci-

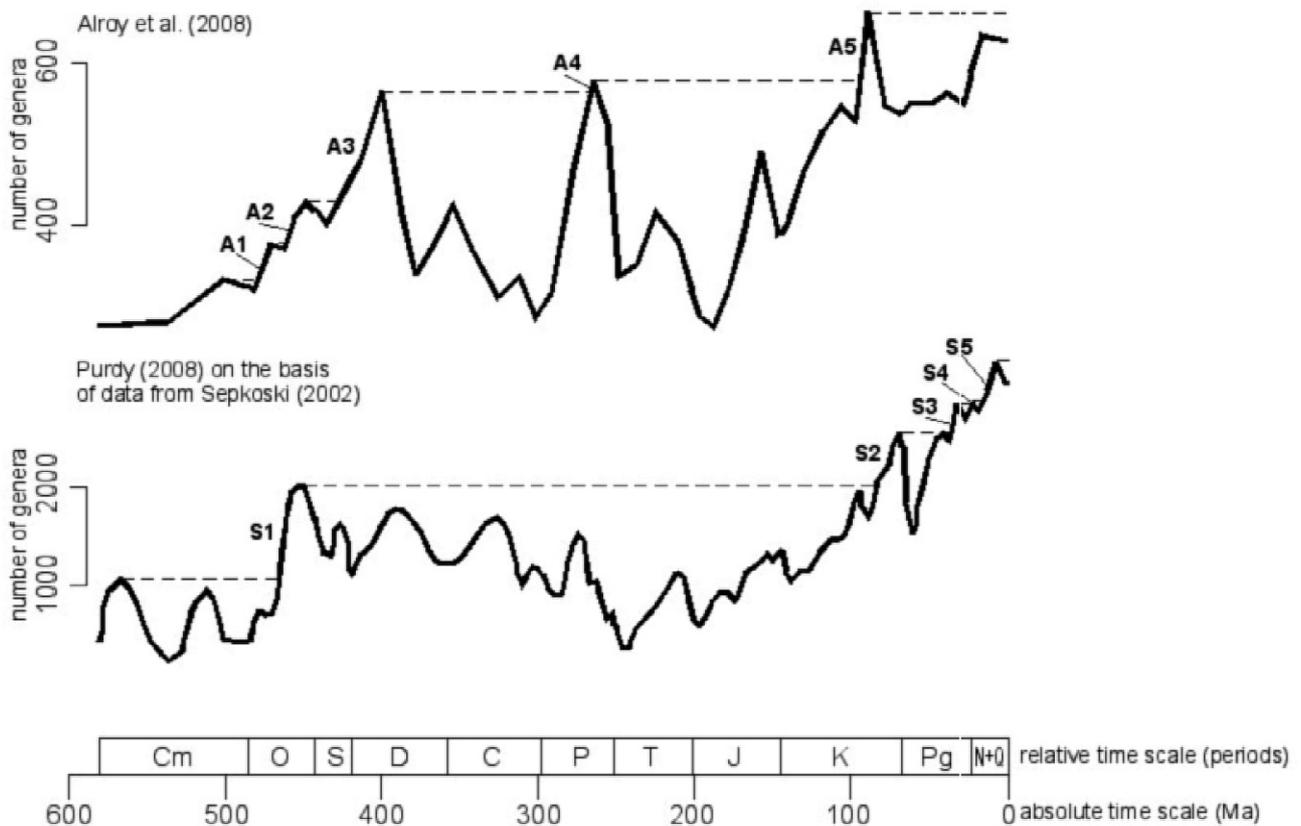


Fig. 2. Alternative curves of the marine biodiversity changes through the Phanerozoic and the relevant interpretations of the marine biodiversity additions. See Tables 1, 2 for more details. Chronostratigraphy follows the latest developments of the International Commission on Stratigraphy (see on-line: stratigraphy.org).

Table 1. Marine biodiversity additions established with the curve of PURDY (2008) on the basis of data from SEPKOSKI (2002).

Abbreviature (see Fig. 2)	Approximate timing	Approximate increase in the total number of taxa relatively to the previous unprecedented level	Correspondence to biotic radiation	Relevant interpretations*
S1	Dapingian–Katian (Middle–Late Ordovician)	+85–95 %	middle and last parts of the Ordovician radiation	major biotic radiation (DROSER <i>et al.</i> 1996; RUBAN 2010, 2013), regional biodiversity peak (KALJO <i>et al.</i> 2011)
S2	Campanian (late Late Cretaceous)	+20–30 %	second half of late Late Cretaceous radiation	threshold for biodiversity (ABERHAN & KIESSLING 2012)
S3	Priabonian (late Eocene)	+10–20 %	middle and last parts of the Priabonian radiation	
S4	Chattian (late Oligocene)	+1%	terminal part of the Chattian radiation	
S5	Burdigalian–Serravallian (mid-Miocene)	+10–20 %	second and last parts of the Early–Middle Miocene radiation	

* In all cases, there was only partial correspondence between the marine biodiversity additions and the earlier-interpreted events.

Table 2. Marine biodiversity additions established with the curve of ALROY *et al.* (2008).

Abbreviature (see Fig. 2)	Approximate timing	Approximate increase in the total number of taxa relatively to the previous unprecedented level	Correspondence to biotic radiation	Relevant interpretations*
A1	Early Ordovician	+5–15 %	first phase of the Ordovician radiation	major biotic radiation (DROSER <i>et al.</i> 1996; RUBAN 2010, 2013)
A2	Middle–Late Ordovician	+10–20 %	second phase of the Ordovician radiation	major biotic radiation (DROSER <i>et al.</i> 1996; RUBAN 2010, 2013), regional biodiversity peak (KALJO <i>et al.</i> 2011)
A3	late Silurian (Ludlow?)–Early Devonian	+25–35 %	middle and last parts of the Silurian–Early Devonian radiation	major biotic radiation (RUBAN 2010), threshold or biodiversity (ABERHAN & KIESSLING 2012)
A4	late Early Permian and/or early Middle Permian	+1–5 %	end of Permian radiation	major biotic radiation (RUBAN 2010)
A5	early Late Cretaceous	+10–20 %	second half of early Late Cretaceous radiation	threshold for biodiversity (ABERHAN & KIESSLING 2012)

* In all cases, there was only partial correspondence between the marine biodiversity additions and the earlier-interpreted events.

dence is not surprising, because it corresponds to the Great Ordovician Biodiversification (DROSER & SHEEHAN 1995; DROSER *et al.* 1996; MILLER & FOOTE

1996; MILLER & CONNOLLY 2001; WEBBY 2001; HARPER 2006; SERVAIS *et al.* 2008, 2009, 2010; MASUDA & EZAKI 2009; RUBAN 2010, 2013). The

absence of coincidence of the other established events (a challenge for the modern palaeobiologists) should be explained by the differences of the original curves of ALROY *et al.* (2008) and PURDY (2008) with regard to the data and the methods employed for their construction.

The both original curves (ALROY *et al.* 2008; PURDY 2008) permit to make some interesting observations. Firstly, the marine biodiversity additions can be subdivided into three categories, namely those that led to significant (up to 90%), moderate (10–30%), and small (~1%) increases in the number of genera. The events of the second category prevailed (Tables 1, 2). However, the cumulative effect of the marine biodiversity additions was very significant. These rare events facilitated increase in the number of genera of marine organisms by several times after the Cambrian. Secondly, the marine biodiversity additions were relatively short-term events, except for the A3 and S1 events (Fig. 2). Thirdly (hypothetically), the marine biodiversity additions occurred in a splash-like mode, and some of them tended to “concentrate” at the 100 Ma-long intervals of the geologic time (Fig. 2). If so, the strength, brevity, and rarity, of the marine biodiversity additions echo the scenario of punctuated equilibrium proposed by ELDREDGE & GOULD (1972) and GOULD (2002, 2007), as well as some general ideas on critical transitions in evolution (SCHEFFER 2009). All above-said underlines the outstanding importance of marine biodiversity additions in the history of life on the Earth. The necessity of their separation from “usual” biotic radiations is also proven.

Yet another interesting observation is worth to made. One would expect that biodiversity additions were only culminations of “usual” biotic radiations, i.e., the former were the only terminal parts of the latter. However, the both biodiversity curves (ALROY *et al.* 2008; PURDY 2008) (Fig. 2) and the interpretations made in this article (Tables 1, 2) do not support this idea. In contrast, the majority of the marine biodiversity additions corresponded to significant parts of the relevant biotic radiations (the S4 and A4 events are exceptions). On the one hand, this observation provides an evidence against “occasional” nature of the marine biodiversity additions. On the other hand, the same observation allows to hypothesize that there was a specific category of biotic radiations that quickly “lifted” biodiversity to new unprecedented levels.

Possible triggers: a general framework for analysis

Various intrinsic (biological) and extrinsic (palaeo-environmental) processes and events, as well as their combinations might have triggered marine biodiversity additions, similarly to how this occurred with “usual” biotic radiations (RUBAN 2010, 2013; ABERHAN & KIESSLING 2012; ABERHAN *et al.* 2012). However, it

should be noted that the former were very peculiar events, because they changed the state of the planetary ecology (see above). Extraordinary forces were required. One should take into account several assumptions. The first assumption is the action of very specific factor(s) influencing the carrying capacity of the global ecosystem at the intervals of the marine biodiversity additions. E.g., the latter might have been triggered by the highest position of the global sea level, extraordinary global warming, etc., i.e., by processes/events that were extraordinary at the interval of the marine biodiversity addition. The second assumption is as follows. If all post-Cambrian marine biodiversity additions were triggered by the same force (or combination of several forces), this force strengthened at the time of the younger additions, because the latter needed more “support” to exceed the previous additions.

The third assumption is that a given marine biodiversity addition requires certain time. It is possible that one extraordinary intrinsic or extrinsic process or event did not necessarily lead to the biodiversity addition if there was not enough time for the relevant acceleration in the number of taxa. Sudden catastrophes (like mass extinctions) or gradual development of unfavourable conditions were able to interrupt a trend towards biodiversity acceleration. As a result, the similarly strong (but not stronger!) trigger repeated later could facilitate diversification above the unprecedented level. In the other words, the potential of each biotic radiation to culminate as a biodiversity addition can be realized either in full or partly. Most probably, more assumptions can be formulated in the same manner. Consideration of them reveals a diversity of models explaining marine biodiversity additions (Fig. 3). Development and further discussion of these models in the light of the available palaeontological and geological data will permit to judge about triggers of the marine biodiversity additions. The complexity of the “Cambrian explosion” (BRASIER 2009; ERWIN & VALENTINE 2013; SANTOSH *et al.* 2014) demonstrates how challenging is this task.

An agenda for further research

This brief article stresses the importance of splash-like marine biodiversity additions in the history of life in the Earth’s seas. However, much work is yet to be done for correct and comprehensive understanding of these events. The urgent tasks for further studies are as follows. Firstly, the new, globally-representative biodiversity curve is required in order to bring the nomenclature of marine biodiversity additions in order. The absence of coherence of the “classical” (PURDY 2008) and “innovative” (ALROY *et al.* 2008) curves is a serious challenge. Achievement of the noted task will also permit to establish the exact duration of each marine biodiversity addition.

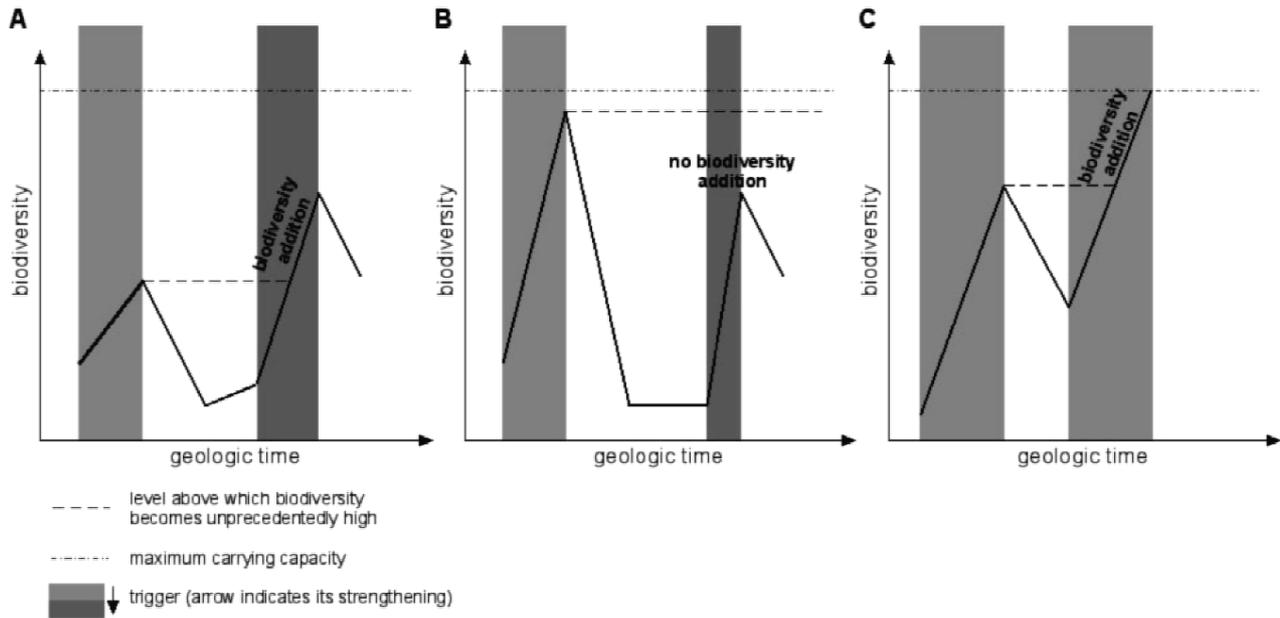


Fig. 3. Selected examples of possible relationships between biodiversity changes and potential single triggers of biodiversity additions. **A**, biodiversity addition as a result of the strengthened trigger. **B**, no biodiversity addition occurred despite the strengthened trigger, because the time, when the latter persisted, was not enough for recovery from the previous biodiversity loss. **C**, biodiversity addition did not require a stronger trigger, because the previous unprecedented level was below the maximum carrying capacity.

Secondly, it should be understood whether marine biodiversity additions involved all or some fossil groups and whether they occurred in all or some regions. A correspondence to coeval events in the evolution of terrestrial biota should be also discussed. Thirdly, a diverse set of models explaining marine biodiversity additions have to be developed and tested, and the assumptions presented above need to be verified. The works of ABERHAN & KIESSLING (2012), ABERHAN *et al.* (2012), and RUBAN (2013) are the first steps in this direction. This third task can be achieved partially by special attention to biological and palaeoenvironmental peculiarities of time intervals of these events and their comparison.

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Резиме

Пост-камбријумско бљесковито увећање морског биодиверзитета

Биодиверзитет морских средина током фенерозоика није био стабилан, а такође се није ни увећавао постепено, већ се одликовао значајним варирањем. Историју морских организама карактерише неколико великих радијација у које спадају и оне које су се дешавале у камбријуму и ордовицијуму. Међутим, многе од ових радијација представљале су само опоравак биодиверзитета који је уследио након катастрофичних догађаја. Због тога је веома важно обратити пажњу на оне временске интервале у којима је морски биодиверзитет достигао више нивое који се раније нису јављали. Оваква радијација (која често представља део веће радијације) могла би се назвати “додатним биодиверзитетом”. Додатни морски биодиверзитет може да се установи на основу графичких анализа “простих” криви биодиверзитета које су одраз целокупног броја таксона и њихових промена кроз геолошко време. Сваки од пет посткамбријских додатних

морских биодиверзитета може се утврдити двома доступним кривима. Помоћу прве криве издвојен је једини додатни марински биодиверзитет у палеозоику, као и серије таквих догађаја током горњег мезозоика и кенозоика. Друга крива указује на “концентрацију” додатних морских биодиверзитета у раном палеозоику, као и на два “раздвојена” догађаја на крају палеозоика и на крају мезозоика. Овакво подударане није изненађујуће с обзиром да одговара великој ордовицијумској биодиверсификацији. Одсуство подударане других већ познатих догађаја може се објаснити разликама оригиналне криве у односу на податке и методе примењених у њиховој реконструкцији. Додатни морски биодиверзитет може бити подељен у три категорије, оне које воде до значајног (до 90%), умереног (10–30%), и слабог (~1%) повећања броја родова. Преовлађују догађаји секундарне категорије. Додатни марински биодиверзитет је релативно краткотрајни догађај са

неколико изузетака. Могло би се очекивати да су додатни биодиверзитети само кулминација “обичне” биотске радијације, тј. да су оне само њихови завршни делови. Међутим, обе биодиверзитетске криве и њихова интерпретација у овом раду не подржавају ову идеју. Насупрот томе, већина додатних морских биодиверзитета одговара значајним деловима одређених биотичких радијација. Различити унутрашњи (биолошки) и спољашњи (утицај палеосредине) процеси и догађаји, као и њихове комбинације могу да изазову додатни морски биодиверзитет, Ипак, требало би нагласити да су поменути догађаји били веома ретки, јер су утицали на промену еколошких услова на читавој планети. Неопходно је установити и пробати различите моделе који би објаснили појаву додатног морског биодиверзитета, а такође је потребно и проверити претпоставку која је овде изнета.

Б. Р.