Splash-like marine biodiversity additions after the Cambrian

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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.

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;
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 any when 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).

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-
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Table 1. Marine biodiversity additions established with the curve of Purdy (2008) on the basis of data from Sepkoski (2002).

| Abbreviation (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 et al. 1996; Ruban 2010, 2013), regional biodiversity peak (Kallo et al. 2011) |
| S2                        | Campanian (late Late Cretaceous)           | +20–30 %                                                                                       | second half of late Late Cretaceous radiation | threshold for biodiversity (Aberian & 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).

| Abbreviation (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 et al. 1996; Ruban 2010, 2013) |
| A2                        | Middle–Late Ordovician | +10–20 %                                                                                       | second phase of the Ordovician radiation | major biotic radiation (Droser et al. 1996; Ruban 2010, 2013), regional biodiversity peak (Kallo et al. 2011) |
| A3                        | late Silurian (Ludlow?)–Early Devonian     | +25–35 %                                                                                       | middle and last parts of the SilurianEarly Devonian radiation | major biotic radiation (Ruban 2010), threshold or biodiversity (Aberian & 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 (Aberian & Kiessling 2012) |

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

Diversity 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).
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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 (SCHIEFFER 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 & KIESLING 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; SANSTOPH 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.
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 also be 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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морских биодиверзитета може се утврдити двема 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 подударање није изненађујуће с обзиром да одговара великој ордовицијумској биодиверсификацији. Одсуство подударања 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, 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 они само њихови завршни делови. Међутим, ове биодиверзитске 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 напласити да су поменути догађаји били веома ретки, јер су утицали на промену еколошких услова на читавој платнети. Неопходно је установити и пробати различите модели који би објаснили појаву додатног морског биодиверзитета, а такође је потребно и проверити претпоставку која је овде изнета.

Б. Р.