

Interactive comment on “The colonization of the oceans by calcifying pelagic algae” by Baptiste Suchéras-Marx et al.

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The comments are organized as :

Comment from R1

→ Our answer with pasted modification in the text and the relevant page and lines modified (or figure).

Dear Editor, The manuscript by Suchéras-Marx et al. presents an interesting compilation of calcareous nannoplankton accumulation rate records through the Jurassic to Neogene. Combined with earlier published compilations of nannofossil species richness and coccolith mean size through this interval, these records provide interesting insights in the macroevolutionary patterns involved in the colonization of the world

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oceans by calcareous nannoplankton. The manuscript is generally well-written and concise, and presents an interesting discussion on the observed evolutionary dynamics.

→ We thank Reviewer 1 for his positive remarks and his constructive review. We have now addressed the main concerns and suggestions. Please find below the detailed responses.

Perhaps the only major point of concern is the geographical limits of the data set. For the Jurassic and Cretaceous (representing a very long time interval, which happens to be crucial for the colonization of the world oceans by calcareous nannoplankton), basically all of the data sets are from the Northern Atlantic & Western Europe. While I realize that the authors are limited by the availability of data sets, I think this is a major weakness of the presented compilation, and a point that is not sufficiently addressed in the manuscript. The authors should include a bit of discussion on the possible problems and/or complications with their data set. How sure are the authors that the Northern Atlantic/Western European records are representative for the global oceans? The authors talk about “open oceans” of the Valanginian, but the Northern Atlantic is still relatively isolated by these times. We know absolutely nothing about the real open oceans (the Pacific & the eastern Tethys). Is it possible that the recorded patterns are diachronous between different ocean basins? I think this merits at least a little bit of discussion, also if the authors do believe they can build a case based on the Northern Atlantic and Western European records alone.

→ We have pondered this point. We highlight this point in section 2.3 and in section 3 (p.8).

Likewise, here and there, the authors oversimplify things a little bit too much, in my opinion. For example, describing the Early Cretaceous to Late Cretaceous, a period of ~60 million years(!), with major pulses of mid ocean spreading, oceanic anoxic events, soaring atmospheric pCO₂ concentrations, major climate shifts, major evolutionary de-

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velopments in many biological groups, as "characterized by a relatively stable environmental setting" is perhaps a bit too simplistic. It feels a bit like a reversed argumentation: "because we see evolutionary patterns that are compatible with the Red Queen macroevolutionary model, the changes in the physical environments must be limited." While I follow the authors in that the influences of the biotic interactions (forcing a Red Queen type evolution) were probably stronger in this time interval compared to the influences of abiotic environmental changes, it is way too simplistic to state that, therefore, the 60 million year period of the Early Cretaceous to Late Cretaceous was characterized by stable environmental conditions: The authors could, and should, rephrase these kind of statements, to incorporate a bit more nuances.

→ We have added a bit of nuance in the section 4 (p.11).

One more thing: I highly recommend using more than one pCO₂ reconstruction for this time interval (the Jurassic to Neogene). The authors have chosen to use the compilation presented in Hönisch et al. (2012) as their sole atmospheric pCO₂ record, while this particular reconstruction seems to underestimate the pCO₂ concentrations for the mid-Cretaceous (a crucial interval for the present study). These kind of problems can be circumvented by using more than one compilation or model based reconstruction, averaging out potential problems with any particular reconstruction.

→ We changed Hönisch et al. 2012 for Foster et al., 2017 and Witkowski et al., 2018 and Meija et al., 2017 (for the Late Miocene) in Fig.2.

To conclude, with a little bit more nuancing and a bit more discussion on the possible problems and pitfalls, this manuscript has the potential to be an important contribution to the field. Therefore, I believe the manuscript merits a publication in Biogeosciences, after some major revisions.

Page 4 Lines 9-15: Is it possible that the recorded patterns are diachronous between different ocean basins? How sure are the authors that the Northern Atlantic/Western European records are representative for the global oceans? I think this merits at least

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a little bit of discussion.

→ This part was actually discussed in SI. Nevertheless, we have now highlighted this point in section 2.3 P4 L19-25 "The vast majority of the samples are from the Northern Hemisphere, and almost all samples for Jurassic and Cretaceous times are from Western Europe outcrops – a relatively poor quantitative record of nannofossils exists outside Europe and in oceanic sites issued from deep-sea drilling programs. Europe, North-Sea, Greenland and North Atlantic represent 81.16% of all compiled samples. Thus, results based on NAR in the Mesozoic will be mostly based on European/Atlantic localities and thus may describe pattern that occurred mainly in the Western Tethys and North Atlantic (see SI S3 and Fig. S3). For the Cenozoic, the data are more widely distributed but the sample per Myr is less abundant than in the Mesozoic (see SI S3 and Fig. S3)."

Figure 2: It is unfortunate that such a large portion of the recorded patterns are forced by the Northern Atlantic/Western European records. Perhaps the authors could color-code the datapoints in A to show the regions where these datapoints are derived from? In addition, I am a bit troubled by the atmospheric CO₂ reconstruction used in this study (based on the compilation in Hönisch et al. 2012). It is odd that the lower Jurassic values are so much higher than the mid-Cretaceous values, while we know that the mid-Cretaceous (Cenomanian-Turonian) was characterized by exceptionally high pCO₂ concentrations. I believe the authors should have a look at some other pCO₂ reconstructions, for example the one recently published by Witkowski et al (2018) in Science Advances; or the modelling work by e.g. Dana Royer. Including more compilations and reconstructions would greatly improve the manuscript.

→ The pCO₂ reconstruction from Hönisch et al., 2012 has been changed in Fig. 2 to Foster et al., 2017 and Witkowski et al., 2018, more recently updated. I have also added Meija et al., 2017 for the Miocene (following Reviewer 2's comment). I would rather prefer not to add modelling works, there are too many solutions deriving from GEOCARB and updated, choosing one would be like choosing the one fitting

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the best. In the new figure showing the NAR, now the "World" is grey and the Europe/NorthAtlantic is in black.

Page 7: Is it possible that these patterns are only representative for the depicted region (the North Atlantic & Western Europe)? Can the authors argue why they believe the patterns in this rather limited (and restricted) region are representative for the global oceans?

→ We cannot demonstrate that the pattern observed is worldwide, the variability in NAR in North Atlantic and western Tethys is so large for a given age, that it might be different in other basins. We changed the text accordingly P8 L14-23 "Hence, this Invasion phase reflects a ~80 Myr-long gradual invasion of western Tethys and Atlantic Oceans by calcareous nannoplankton during the Jurassic-Early Cretaceous time interval. According to coccolith biometric data, the *Watznaueria barnesiae* (i.e. a cosmopolitan Mesozoic coccolithophore species) genetic flux was maintained between populations in the western Tethys and in the eastern Panthalassa in the Lower Cretaceous likely related to circum-global circulation (Gollain et al., 2019) through the Tethys. The Early Cretaceous Invasion phase observed in the Atlantic Ocean may have thus happened in all open oceans realms worldwide, although our restricted European/North Hemisphere dataset cannot corroborate it."

Page 7 Line 3: I am not familiar with the term "Viking Corridor". Can the authors explain this? Or provide a reference to a study that does?

→ The Viking Corridor (Wertermann, 1993) or Viking Strait (Callomon, 1985) is the name of the connection between Boreal Sea and Northern Western Tethys and it is commonly used (e.g. Aberhan, 2001; Dera et al., 2009; Korte et al., 2015; Ruebsam et al., 2014). We have now added Westerman, 1993 reference in the text.

Page 7 line 7: in the record of Aubry et al. (2005), the coccolith size actually already starts increasing in the Late Jurassic. In addition, I wonder, why would Cope-Depéret's rule not yet be in place in the Middle Jurassic?

→ A small increase in the size trend starts around the J/K boundary. Hence, a net increase in size is observed since the base of the Early Cretaceous. The reason why the Cope-Deperet's rule does not apply to earlier times (e.g., the middle Jurassic) stays thus unclear. We have now added precisions in the text P8 L25-27 "From this point up to the end of the Cretaceous, NAR remained high but the nannofossil species-richness and the coccolith mean size increased since the beginning of the Cretaceous following the Cope-Depéret's rule (i.e. increase in size over evolutionary time; Aubry et al., 2005)."

Page 7 Lines 10-11 "Hence, this Invasion phase reflects a ~80 Myr-long gradual invasion of world open oceans by calcareous nannoplankton during the Jurassic-Early Cretaceous time interval." => It is interesting to see how the radiation/invasion over this interval directly and indirectly, led to a proliferation of various benthic groups such as burying and swimming crabs and irregular echinoids as well as nektonic groups such as ancyloceratine heteromorph ammonites. See the study of Fraaije et al (2018) for this. Perhaps worth mentioning?

→ We don't mention it in the results but we have now added it in fused Discussion (i.e. fusion of former sections 4.1 and 4.2) P12 L18-21 " Ultimately, the Mesozoic Plankton Revolution led to a bottom-up control of plankton on the entire marine ecosystem structure (Knoll and Follows, 2016), as revealed by the diversification of spatangoids echinoids, palaeocorystids crabs, Ancyloceratina ammonites (Fraaije et al., 2018) and many other groups during the Mesozoic Marine Revolution (Vermeij, 1977) including highly diverse marine reptiles (Pyenson et al., 2014)."

Page 7 Lines 16-17: can the authors elaborate a little bit more on which type of specializations they are talking here? Which kind of ecological conditions?

→ We have now changed these lines accordingly into P8 L29-30 "This phase corresponds to a Specialization phase, where more and more species shared an increasingly filled ecospace through specialization to particular ecological niches." This point

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is more developed in the Discussion later in the text P12 L6-9 "This specialization might correspond to an adaptation of different species to a particular ecological niche, to variable trophic levels (i.e., oligo- to eutrophic; e.g., Herrle, 2003; Lees et al., 2005), or temperature conditions (e.g. Mutterlose et al., 2014), or seasonality and blooming (e.g. Thomsen, 1989)."

Page 7 lines 22-23: How does this work? What forces this "establishment phase"? I see that the authors discuss this topic further on in the manuscript, but in its current form, this sentence triggers the big "why?" question. Why did less species, with smaller sizes, dominate? What forces this?

→ We have now considered the possible reasons for this pattern and added discussion in the Discussion P13 L1-15. Following R2, the discussion has been thoroughly revised, by merging both sections 4.1 and 4.2. In the new version of the MS, the establishment phase is discussed in the last paragraph.

Page 9 Line 28 "within less than..": this "within" feels a bit superfluous. Maybe just "in less than.."?

→ corrected accordingly.

Page 9 Line 32: Why is "Specialization" capitalized here?

→ it shouldn't, corrected.

Page 10 Lines 15-22 "This phase was not related to major physical or chemical changes, climatic and environmental parameters showing steady-state dynamics": With major pulses of mid ocean spreading, oceanic anoxic events, soaring pCO₂ concentrations, major climate shifts, major evolutionary developments in many biological groups, the Early Cretaceous to Late Cretaceous, a period of ~60 million years (!), can hardly be called "a relatively stable environmental setting". I suggest the authors rephrase this paragraph.

→ corrected P12 L10-13 "This time interval witnessed many short-term climatic and

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environmental perturbations such as OAEs, thermal optimums or cooling (Friedrich et al., 2012), but also some relatively stable long-term physical conditions (e.g., sea-level; Müller et al., 2008)."

Page 10 Lines 22-23: => this bottom-up control of the marine ecosystem structuration also led to the emergence and dispersion in the different higher-tier trophic levels, discussed earlier (Fraaije et al. 2018).

→ We have now added P12 L18-21 " Ultimately, the Mesozoic Plankton Revolution led to a bottom-up control of plankton on the entire marine ecosystem structure (Knoll and Follows, 2016), as revealed by the diversification of spatangoids echinoids, palaeocystids crabs, Ancyloceratina ammonites (Fraaije et al., 2018) and many other groups during the Mesozoic Marine Revolution (Vermeij, 1977) including highly diverse marine reptiles (Pyenson et al., 2014)."

Page 11 Lines 3-4: Perhaps the authors can elaborate a little on why the diatoms diversified over this time interval? This group appears to have shown an adaptive radiation tied to higher dissolved silica concentrations and stronger circulation and upwelling from the mid-Cenozoic onwards (Falkowski et al., 2004).

→ We follow the latest argumentation about silicic acid input to the oceans (Cermeño, Falkowski et al., 2015 PNAS) P13 L9-10 "Secondly, diatoms tremendously diversified due to increase in silicic acid input to the oceans during this time interval (Spencer-Cervato, 1999; Cermeño et al., 2015) [. . .]"

Page 11, Lines 15-16 "The first phase, Early Jurassic to Early Cretaceous, corresponds to the nannoplankton oceans' Invasion marked by an increase in NAR and in species richness along with a quite steady coccolith mean size." This sentence is difficult to follow. Please rewrite.

→ We changed for P13 L22-24 "The first phase from Early Jurassic to Early Cretaceous, corresponds to the nannoplankton oceans' Invasion. This phase is marked by

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an increase in NAR and in species richness along with steady to slight increase in coccolith mean size."

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