Answer to reviewers by Baptiste Suchéras-Marx about the manuscript entitled “The colonization of the oceans by calcifying pelagic algae”.

Reviewer 1:

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 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 developments in many biological groups, as "characterized by a relatively stable environmental setting” is perhaps a bit to 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 to 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 there 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 Mejia 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 manuscript merits a publication in Biogeosciences, after some major revisions.

Page 4 Lines 9-15: Is it possible that the recorded patters 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 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 pCO_2 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 Mejia 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 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 cosmopolitain 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 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 "establishement 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 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, 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 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 an increase in NAR and in species richness along with steady to slight increase in coccolith mean size."

Reviewer 2:
The manuscript "The colonization of the oceans by calcifying pelagic algae" by B. Sucheras-Marx et al. describes colonization of the oceans by coccolithophorids since the last 200 M. This well written manuscript is based on the compilation of nannoplankton accumulation rates in sediments, brought in context with previously published species richness, coccolith size as well as atmospheric CO2. Results indicate a colonization of the oceans in distinct phases, shaped by the reproduction strategy, interactions with other planktonic organisms and the physical environment.
The research is original and provides interesting findings to the community. The data set compilation seems to have been carried out with great care, even though, sadly, the available data is confined largely to the Atlantic, therefore I would suggest to maybe rephrase the main conclusions of the manuscript from "World Oceans" to "Atlantic". The manuscript is concisely written, however, could benefit from a re-organization of the Discussion paragraph in my opinion, so that each phase is discussed in its own paragraph, instead of discussing the colonization twice in 4.1 and 4.2.
→ We thank Reviewer 2 for her positive comments. Following the R2's remarks, we have now merged sections 4.1 and 4.2 and re-organized the Discussion by paragraphs, the first one introducing the models, andthe following ones describing each phase in a separate paragraph.

I have some reservations regarding the smoothing of the NAR and the seemingly arbitrary reference to sometimes the smoothed trend and sometimes the underlying raw data. The authors should carefully re-examine each time the NAR is discussed and elaborate on when which datatype is discussed (see major comments below).

I would recommend publication of this manuscript after minor revisions have been carried out. I wish the authors good luck with the revisions and remain available for further feedback and discussions.

Please see my comments below (p=page, l=line):
Major comments:
NAR calculation: Since the majority of the manuscript hinges on the NAR, it would be great if the authors could provide an propagation of error for the NAR values, as they are calculated from 3 other variables. Additionally the NAR in Fig. 2 has a high variability of several orders of magnitude, can the authors elaborate on this a bit, e.g. is this caused by pooling different ocean locations, where changes could have happened at a different point in time?
→ We strongly agree with R2's remarks, I am myself fighting for more control on uncertainties in Earth Sciences in general (see as an example Suchéras-Marx et al., in revision at Marine Micropaleontology titled "Statistical confidence intervals for relative abundances and abundance-based ratios: simple practical solutions for an old overlooked question"). Unfortunately, in the present case, we cannot propagate uncertainties simply because the original publications do not provide information on the counting uncertainties, stratigraphic uncertainties or density. Thus, propagation would be completely arbitrary and may suggest to the reader that we control uncertainties, which is unfortunately not true.

Smoothed curve versus raw data: Currently, in some time periods smoothed NAR values are discussed and sometimes the raw data. Please state each time, which data is taken (raw data or smoothed trend). Please be careful in not mixing the two.
e.g. p9 l29 " a steady production for the rest of the epoch" seem to be rather subjective, as there seems to be rather a huge variability in observed NAR post K-Pg until the end of the Paleocene, just the chosen smoothing factor results in a steady NAR. How have the authors assessed "stable phases" in NAR versus "changing phases" of NAR? Only by visual observation of the smoothed trend?
→ Yes, we do not calculate any test for that, we prefer to directly observe the curve and compare it to the other ones.
By just looking at the smoothed curve, variability in the NAR data is lost. While I agree that in some time points a SF of 0.1 is influenced by the sampling resolution, however, in other time points variability and trends are lost by a higher smoothing factor (e.g. the increase in NAR since the middle Paleogene, which is "smoothed away" otherwise). Furthermore (p9 l27) here the average NAR shows no change during the K/Pg event, but NAR clearly changes, which is also discussed.

→ R2 is right. In the new version of our MS, we now state when the raw NAR or the smooth NAR is considered.

Layout Figure 2: please mark the individual colonization phases in a way, that they are easy to be put into context with the NAR record. Currently, the phases are indicated on the far right and the NAR record is on the far left, making it hard to see the exact phase changes. I would suggest shading of the background. Please also indicate the Torcian and Valangian. And add a line for the K-Pg event, as some of the statements (e.g. p9 l28 " ..the NAR recovered to pre-extinction levels within less than 4 Myr") are hard to follow with the current Figure layout.
→ Fig. 2 has been largely amended following R1 and R2 comments.

Minor Comments:
p2 l2: represent (without s)
→ corrected

p2 l6-13: also refer to the Kuenen Event in the discussion or remove from Introduction
→ the Kuenen Event is the shift from carbonate system dominated by neritic production from benthic organisms to pelagic production from planktic organisms. Hence it is crucial to cite this event in the Introduction because it is linked to planktic organisms' evolution. But because we don't quantify carbonate in this study, we cannot speculate on the timing of this event thus we don't discuss it. We have made some modification in the text to derive the point from Kuenen to evolution transition P1 L7-16 "There is then a transition from Jurassic calcareous nannofossil-poor to Late Cretaceous and Cenozoic calcareous nannofossil-rich oceanic sediments which has shifted the carbonate accumulation in neritic environment by benthic organisms to accumulation in pelagic environments by planktic organisms. This major carbonate system change is known as the Kuenen Event (Roth, 1989), and has been referred to a tectonically-mediated intensification of the ocean circulation. This event is concomitant with the development of several planktic groups (e.g., planktic foraminifera (Hart et al., 2003), diatoms (Kooistra et al., 2007)), may be seen as a Mesozoic Plankton Revolution (derived from Vermeij, 1977) and thus is also dramatically related to plankton evolution. The causes and consequences of this biotic revolution have been extensively discussed, but the transition itself remains poorly documented; most interpretations solely rely on species richness (Falkowski et al., 2004; Knoll and Follows, 2016), which does not provide an exhaustive framework to fully appreciate the evolutionary history of calcareous nannoplankton."

p3 l17 mm2
→ corrected.

p4 Fig. 1 caption: type of outcrop: rephrase outcrop; deep sea drilling is not an outcrop
→ corrected.

p5 l5: SI= suppl. inform. (define)
→ corrected.

p7 l 6: I would structure the paragraph according to the different phases, e.g. add a break in the middle of l. 6.
→ corrected.

p7 l 14: regarding the versatile readership of BGD, I would refrain from using too many specific terms such as Cope-Deperets rule, which are not explained in the Introduction, same for Margalefs mandala in p9 l12, also explain briefly K and r strategists (for readers from a more geological background).
→ corrected; we have also added short precision of each specific terms listed above P8 L27 "[…] Cope-Depéret's rule (i.e. increase in size over evolutionary time; Aubry et al., 2005)"; P11 L11-12 "(i.e. Fig. 2 from Margalef, 1978)"; P11 L12-15 "between K- (corresponding to organisms evolving in more stable, predicable and saturated environments) and r- (organisms living in unstable, non-predictable, and unsaturated environments) strategists (Reznick et al., 2002), living in intermediate

nutrient-concentration waters, turbulence and light availability (Margalef, 1978; Balch, 2004; Tozzi et al., 2004)."

p7 l 17: ecospace or ecological niche?
→ ecospace.

p7 l 24: dominance: rephrase, as modern oceans are not dominated by Ehux, but it is the dominant cocco?
→ rephrased P9 L2-4 "This Establishment phase reached a climax in modern oceans with the dominance within the coccolithophore community of the iconic small-sized species *Emiliania huxleyi* (e.g. Ziveri et al., 2000; Baumann et al., 2004)."

p8 Fig 3: please add also a time stamp to panel c (Valanginian?)
→ slight modification of the Fig. 3 with a stratigraphic column.

p9: when the term species is used, calc. nannoplankton species is meant? Or coccolithophorids?
→ calcareous nannoplankton, the term is added to species when needed.

p 9: I find the terms R-pole and K-pole confusing, are these commonly used terms? Or do they just hint towards the respective areas in Margalefs mandala?
→ r- and K- strategists is a common term in ecology. We slightly modified it to highlight the fact that within plankton, calcareous nannoplankton are intermediate strategist and within calcareous nannoplankton there are species that are closer to one or the other side or "*pole*". We have now modified these lines to P11 L24-25 "Hence, the ecology of Jurassic-Early Cretaceous nannoplankton species was closer to the "*r-strategist*" pole of density-independent selection (Reznick et al., 2002). […] P12 L9-10 Consequently, late Early and Late Cretaceous species were closer to the "*K-strategist*" pole of density-dependent selection, corresponding to organisms evolving closer to carrying capacity."

p9 l21: the maximum occurs much later, this need to be rephrased.
→ The sentence p9 l21 is: "It suggests that more and more species shared an increasingly filled ecospace (Fig. 2), therefore becoming more specialized to peculiar environmental conditions." I am sorry but I don't understand what R2 means.

p9 l24: please explain "roughly stable"
→ bad writing. Modified for "The raw NAR reached an optimum at ~133 Ma and the smooth NAR is flat from ~117 Ma until the K–Pg mass extinction event (66 Ma), which had a catastrophic impact on calcareous nannoplankton diversity with a species turnover up to 80 % during the crisis (Bown, 2005)."

p9 l. 32: where is the "ecological specialization" seen in the data?
→ the specialization is not seen in data per say but inferred based on the observation that more species sharing the same ecospace are producing a stable number of individuals. If the ecospace is split between more species, then the species must be more specialized to peculiar conditions.

p10 l10: What are "red lineage algae"? Those belonging to the Red Queen Model?
→ the red lineage algae are those using chlorophyll c and derivatives as accessory pigments. Added in text P11 L31-33 "[…] red lineage algae (i.e. using chlorophylle a, with chlorophylle c and fucoxanthin as accessory pigments typical in Haptophyte) such as coccolithophores (Falkowski et al., 2004)"

p10 l 18 - 20: please add citations.
→ citations added P12 L14-17 "This time interval is the paroxysm of the *Mesozoic Plankton Revolution* with the first occurrence of diatoms, a plateau of marine dinoflagellate species-richness, and the diversification of planktic foraminifera which, together with calcareous nannoplankton (Falkowski et al., 2004; Knoll and Follows, 2016), contributed to form massive chalk deposits (Roth, 1986)."

p 10 l 28: where is the "post crisis Invasion period" in Fig 2?
→ we can't see it, we just speculate it must be one since the diversity and nannoplankton productivity dramatically dropped at the K-Pg boundary. We have added precision in the following P12 L29-32 "At a much shorter time-scale, the Paleocene appears therefore similar to the Jurassic-Cretaceous interval in that a first Invasion phase (the post-crisis biotic recovery) and the origination of new calcareous nannoplankton families (Bown, 2005) is followed by a period of species diversification and ecological specialization – a Specialization phase."

p10 l 31: "smaller sized species than in the Mesozoic": to me it looks like the average coccolith size is relatively the same between this period and the Jurassic portion of the Mesozoicum.
→ modified to "Cretaceous".

p11 l 1 The "decrease in pCO2" during the Neogene is not visible in Fig2, maybe another dataset would be more suitable? Also, how do the authors then explain the stable coccolith mean size and increasing NAR during the Jurassic, where pCO2 showed the largest drop?
→ Firstly, the Bolton's model is based on reaching an unknown threshold in pCO_2 during the Miocene with pCO_2 too low to sustain CO_2 diffusion through the cell wall for both organic and inorganic carbon fixation in large coccolithophore cell. The Lower Jurassic decrease just not reach this threshold. We have added P13 L4 "below a threshold" to the sentence. Secondly, the Miocene pCO_2 discussion is really critical and controversial between specialists. In order to overcome this issue we have changed Hönisch's data compilation in Fig.2 to Foster's data compilation (which is really similar but more recent), added Witkowski et al. 2018 data (asked by R1) and added in grey Mejia et al. 2017 results (range due to uncertainties) which record the Miocene pCO2 decrease.