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10 To: *Biogeosciences*, editorial board

11
12 Leuven, October 11th 2016

13
14 Dear Editor,

15
16 Herewith we like to resubmit our manuscript on the ecological responses to the collapse of the
17 biological pump following the K-Pg boundary impact.

18
19 Please find attached a revised version of our manuscript entitled "***Ecological response to***
20 ***collapse of the biological pump following the mass extinction at the Cretaceous-Paleogene***
21 ***boundary***", submitted by J. Vellekoop, L. Woelders, S. Açıkalın, J. Smit, B. van de Schootbrugge,
22 I.Ö. Yilmaz, H. Brinkhuis and R.P. Speijer.

23
24 We thank the two reviewers for their valuable comments and suggestions, which have been very
25 helpful in improving our manuscript. After thorough revisions, we believe that we will convince
26 the reviewers of our main conclusions.

27
28 The relative minor and constructive comments by the first reviewer, Lee Kump, were almost all
29 incorporated in the revised manuscript. Below, we include a general reply to the comments
30 provided by Reviewer 1.

31
32 The second reviewer, Flavia Boscola Galazzo, raised more substantial comments, regarding the
33 interpretation of the benthic foraminiferal data and the comparison between different
34 foraminiferal records. In our revised manuscript, we have clarified several issues that clearly
35 raised confusion and have improved several figures, as suggested by this reviewer.

36
37 Below, we include a point-by-point reply to both reviewers. We hope that by addressing all of the
38 points raised by the reviewers and improving our manuscript accordingly, you are able to
39 reconsider this manuscript for publication in *Biogeosciences*.

40
41 Looking forward to your decision on our manuscript, with best regards,

42
43 Johan Vellekoop

44 Signed on behalf of all the authors

45

1 Below follows a point-by-point response to the comments by the reviewers. Comments
2 by the reviewer are **in bold**, our reply is in normal font.

5
6 **COMMENTS BY LEE KUMP**

9 **[A good citation for this is Hilting et al., 2008, "Variations in the oceanic vertical
10 carbon isotope gradient and their implications for the Paleocene-Eocene
11 biological pump", *Paleoceanography* 23:doi:10.1029/2007PA001458..]**

12
13 ---

14 We have now incorporated this citation in our revised manuscript.

16 **[The authors don't really have any direct evidence that the biological pump
17 collapsed at their site, because they have no benthic d13C values. If they could
18 generate these data their story would be further substantiated.]**

19 -----

20 We agree with the reviewer that obtaining a benthic foraminiferal $\delta^{13}\text{C}$ record would
21 further substantiate our otherwise indirect evidence that the efficiency of the biological
22 pump decreased at our study sites. However, given the poor preservation of carbonate
23 in our records, with all foraminifera showing full recrystallization, it not feasible to
24 generate a reliable benthic foraminiferal $\delta^{13}\text{C}$ record for the Okçular section.

25 Nevertheless, although we not have the direct evidence that a benthic foraminiferal $\delta^{13}\text{C}$
26 record would have provided, our records do show an increase in nutrient availability in
27 the surface oceans, whilst there is a decrease in food supply at the sea floor. This
28 suggests a causal link, i.e. a reduction of the transport of organic matter from the surface
29 ocean to the sea floor (=a reduced biological pump strength), resulting from a decreased
30 fraction or the organic matter produced photic zone is transported down.

31
32 Moreover, if it is true that the collapse of the biological pump at the K-Pg boundary is a
33 consequence of the ecosystem reorganization that resulted from the mass extinction, it
34 is to be expected that this also occurred at the Okçular section, since these extinctions
35 occurred on a global scale. Therefore, we consider it very likely that the Okçular section
36 represents a similar system response as previously studied sites in the Tethys.

38 **[The collapse of the biological pump should indeed lead to enhanced nutrient
39 recycling into the photic zone and should also expand and shoal the oxygen
40 minimum zone. The authors might want to consider this in light of their
41 interpretations of indicators (or lack thereof) of dysoxia at various sites.]**

1 -----

2 We agree with the reviewer that it is likely that the enhanced nutrient recycling in the
3 photic zone should lead to an expansion of the oxygen minimum zone. In particular,
4 when there is a reduction of transport of organic matter out of the photic zone, and,
5 hence, more remineralization in the photic zone itself, it is to be expected that the
6 oxygen minimum zone will shoal. It is therefore not unimaginable that the low-diversity
7 benthic foraminiferal assemblages in P0 in our study sites might also be influenced by
8 lower oxygen concentrations. However, in contrast to some other sites (e.g. Coccioni and
9 Galeotti, 1994; Kaiho et al., 1999), there is no other evidence from the sites investigated
10 here pointing towards truly hypoxic conditions. Therefore, in our study, we cannot make
11 any firm conclusions on this matter.

12

13 It is important to realize that minimal oxygen concentrations in oxygen minimum zones
14 depend on a large variety of factors, and therefore, at different locations, oxygen
15 minimum zones can have very different minimal oxygen concentrations, ranging from 0
16 ml l⁻¹ at some extreme sites, to up to barely below 5 ml l⁻¹. Although it is very well
17 possible that oxygen concentrations decreased at the seafloor, this decrease would not
18 necessarily have to result in hypoxic conditions at our study sites. It is therefore possible
19 that such a decrease in oxygen availability was not reflected in the benthic foraminiferal
20 assemblages.

21

22 We have now included a sentence in the manuscript discussing the possible shoaling of
23 the oxygen minimum zone as a consequence of nutrient recycling in the upper part of
24 the water column (page 10, lines 4-6).

25

26 **[I think the contrasting behavior in the open ocean (deep sea), e.g., page 12,**
27 **paragraph beginning line 24, can be understood by the relative resistance of the**
28 **more recalcitrant organic matter that the deep sea usually gets anyway to more**
29 **intense surface ocean recycling with the collapse of the biological pump. In other**
30 **words, the deep-sea benthic foraminifera continue to receive recalcitrant organic**
31 **matter at barely diminished rates despite the collapse of the biological pump.]**

32

33 We thank the reviewer for this valuable suggestion. This idea might provide a very good
34 alternative hypothesis for explaining the observed differences between the signal at
35 most continental margin sites versus the signal at Shatsky Rise. We will include a brief
36 section discussing this alternative hypothesis (page 12, lines 15-19).

37

38 **[Page 1, Line 16: I think the "now unequivocally shown. . ." comment about impact**
39 **as the cause of the extinction should be removed; the comment is irrelevant to the**
40 **current manuscript and might be considered by some as a "pot shot" at the**
41 **volcanic origin idea. The way this same idea is put on line 31 is better "It is now**
42 **commonly accepted. . ."]**

43 -----

44 We agree and have now adjusted this sentence in our manuscript accordingly.

45

46 **[Page 2, Line 12: My modeling did not suggest that "productivity had to continue**
47 **nearly unabated . . . (Kump, 1991). Rather it showed that burial had to continue**
48 **nearly unabated. Burial could have been in shallow water or on land, where the**
49 **required productivity would not impact the ocean's vertical carbon isotope**

1 **gradient. Primary productivity certainly COULD have continued unabated, but**
2 **export productivity had to have been diminished (unless the whole ocean became**
3 **destratified and well-mixed).]**

4 -----

5 We agree and have adjust this paragraph in our manuscript accordingly.

7 **[Line 14: "persistence"]**

8 ----

9 OK, corrected.

11 **[Line 22: remove "to" after "from the photic zone"]**

12 ----

13 OK, corrected.

16 **[Page 3, Line 17: "changes in, for example, temperature . . . "]**

17 ----

18 OK, corrected.

21 **[Page 4, line 14: Might be good to foreshadow the main conclusions at end of this**
22 **Paragraph.]**

23 ----

24 Although we understand and appreciate the suggestion by the reviewer, we feel that
25 foreshadowing the main conclusions at the end of the introduction would give the
26 impression that we were biased towards the outcome of this study. We therefore do not
27 consider this the most elegant approach.

30 **[Page 5, line 18: "quantitative" ?]**

31 ----

32 We thank the reviewer for pointing out this error in our manuscript. The correct term
33 should indeed be "quantitative".

36 **[Line 22: indicative "of"]**

37 ----

38 OK, corrected.

41 **[Page 6, Line 1: data "were"]**

42 ----

43 OK, corrected.

46 **[Page 12, line 22: some of the effects of the impact, like the trace-metal poisoning,**
47 **could have been relatively long-lived. See for example Jiang et al. Nature**
48 **Geoscience 3, 280 - 285 (2010).]**

1 ----

2 The reviewer is correct that, in the worst-case scenario of Jiang et al. (2010), trace-metal
3 poisoning could have lasted for up to 10 kyrs. However, this is assuming the worst-case
4 scenario (i.e. assuming 100% metal solubility). When more realistic metal solubilities
5 are assumed (1% solubility), the duration of a possible trace-metal poisoning is
6 considerably reduced, i.e. to 1 kyr (Jiang et al., 2010, supplementary material). This,
7 indeed, is considerably longer than for example the duration of the hypothesized impact
8 winter, but still relatively short-lived compared to the long-term biological and
9 paleoceanographic reorganizations that occurred after the K-Pg boundary mass-
10 extinctions, which occurred over hundreds of thousands of years.

11

12

13

14

15

16 **COMMENTS BY FLAVIA BOSCOLA GALAZZO**

17

18

19 **[Research approach: it should be kept independent from the main models (e.g.**
20 **Living Ocean model, see comment below) concerning the K/Pg marine biological**
21 **crisis. The already known models must not be used to interpret the data,**
22 **differently the reasoning gets circular preventing any new knowledge from**
23 **emerging.]**

24 --

25 We disagree with the reviewer here. Naturally, the benthic foraminiferal and dinocyst
26 data were obtained and analyzed 'independent from the main models'. However, when
27 interpreting the obtained results, it is, in our opinion, crucial to view the results in the
28 context of known models.

29 It should be noted that, although in the past decades there has been a considerable
30 debate on the occurrence of a collapse of the biological pump following the K-Pg
31 boundary mass extinction (e.g. Alegret and Thomas, 2009), almost all recent studies are
32 in agreement that post-K/Pg export productivity was reduced *to some extent*. Current
33 discussions mostly involve discussions on the *severity* of the reduction of export
34 productivity, or on the geographical differences (i.e. the 'heterogeneity' of the oceans).
35 Even studies that argue for a more 'heterogenic' response of the global marine
36 ecosystems, such as Esmerey-Senlet et al (2015) argue that, although there was spatial
37 heterogeneity in the wake of the K/Pg mass extinction, "*the interbasinal $\delta^{13}C$ gradient*
38 *was reduced after the mass extinction, suggesting a reduction in global export*
39 *productivity*".

40 Moreover, while records from for example the open Pacific Ocean could, potentially, be
41 explained as showing no reduction of the biological pump (e.g. Alegret and Thomas,
42 2009; Alegret et al., 2012), there is no discussion on the occurrence of a collapse of a
43 biological pump in the Tethys Ocean, Atlantic Ocean, Southern Ocean and Indian Ocean (e.g.
44 following Thomas, 1990; Olsson et al., 1996; Hull et al., 2011; Alegret et al., 2012). We

1 therefore do not see it as the target of our study to ‘test’ the living ocean model. Instead,
2 given that it has been convincingly shown that this model is valid for the Tethys (e.g.
3 Hull et al., 2011; Alegret et al., 2012, etc.), the main focus region of this study, the
4 objective of this study was to investigate the potential ecological consequences of this
5 early Danian ‘living ocean’ condition.

6 To clarify these issues, we have now included a paragraph on this matter (page 2, lines
7 23-31).

8

9 **1. [Title: The model arguing for a global collapse of the biological pump following**
10 **the mass extinction is controversial, and still not univocally accepted (see**
11 **Thomas, 2007, Birch et al., 2016). I suggest to the authors to remove it from the**
12 **title.]**

13 --

14 Most recent studies are in agreement that, *at most sites*, export productivity was
15 reduced *to some extent*. Also the reference cited by the reviewer (Birch et al., 2016
16 “Partial collapse of the marine carbon pump after the Cretaceous-Paleogene
17 boundary”), states “*Our results show that changes in ocean circulation and*
18 *foraminiferal vital effects contribute to but cannot explain all of the observed collapse*
19 *in surface to deep-ocean foraminiferal $\delta^{13}C$ gradient. We conclude that the biological*
20 *pump was weakened as a consequence of marine extinctions, but less severely and for a*
21 *shorter duration (maximum of 1.77 m.y.) than has previously been suggested.*”

22 Indeed, there have been discussions on the geographical heterogeneity of the oceanic
23 response (Hull et al., 2011; Alegret et al., 2012). However, even studies that argue for
24 a more ‘heterogenic’ response of the global marine ecosystems, such as Esmerey-
25 Senlet et al (2015) argue that, although there was spatial heterogeneity in the wake
26 of the K/Pg mass extinction, “*the interbasinal $\delta^{13}C$ gradient was reduced after the*
27 *mass extinction, suggesting a reduction in global export productivity*” and that there is
28 convincing evidence for a collapse of a biological pump in the Tethys Ocean, Atlantic
29 Ocean, Southern Ocean and Indian Ocean (e.g. Hull et al., 2011) Therefore, using
30 benthic foraminiferal and dinocyst records from these regions (not the Pacific) can
31 be used to assess the ecological response to the collapse of the biological pump in
32 these regions. Therefore, we argue that it is valid to use this term in our title.

33

34 **2. [Introduction: Pag. 4-L9-13: this paragraph states the approach of this paper**
35 **which in my opinion is conceptually wrong. You don’t do carry out a new**
36 **research to place it “in the context” of what it is already known or thought to be**
37 **known, but to bring in new knowledge, improve, edit or discard what’s already**
38 **known.]**

1 --

2 We agree with the reviewer that 'placing in the context' is not a goal on itself. Naturally,
3 this was not the goal of this study. Therefore, we have rewritten this section accordingly.

4

5 **3. [Methods: The authors studied the size fraction larger than 125 μm for the**
6 **benthic foraminiferal analysis. This can lead to miss important ecological**
7 **information as disas- ter taxa and stress tolerant opportunistic taxa which**
8 **bloom during environmental stress are often smaller (e.g., Boscolo Galazzo et**
9 **al., 2013; Giusberti et al., 2016). To me the use of the >63 μm size fraction**
10 **would have been more appropriate for this study. See for instance Thomas**
11 **(1990), Alegret et al. (2003), Alegret and Thomas (2007; 2009). The study of**
12 **the smaller size fraction might for instance reveal peaks of small opportunistic**
13 **infaunals, challenging the current environmental interpretation. Ideally the**
14 **counts should be improved counting the whole >63 μm size fraction. I**
15 **understand that at this stage this would imply the re-study of the whole sample**
16 **set. However, the authors should at least re-count same samples using the**
17 **whole >63 μm size fraction in order to check that important ecological**
18 **information/patterns are not missed in the critical stratigraphic intervals with**
19 **the use of the larger size fraction. These additional data should be included as**
20 **a figure in the paper.]**

21 --

22 We fully agree with the reviewer that studying the size fraction >63 μm is generally
23 preferable, especially in deep-sea environments with many small taxa. However, the
24 preservation of the studied material from Okçular is rather poor, resulting from strong
25 recrystallization during deep burial of the sequence. Already in the >125 μm size
26 fraction, accurate determination of foraminifera even to the genus level was often
27 difficult. This resulted in a relatively high 'Indet.' group. A study on the smaller size
28 fraction would provide better insight into the abundance of small taxa, yet this would go
29 hand in hand with an even higher indeterminable fraction, further compromising an
30 accurate portrayal of the benthic foraminiferal assemblage. It should be noted that the
31 comparative data of the similar but much better preserved material of El Kef is also
32 based on the >125 μm fraction.

33 Furthermore, we are not fully convinced that the choice of size fraction necessarily
34 influences the overall patterns significantly. This is exemplified by the study performed
35 on the PETM by Ernst et al. (2006). In this study, the authors compared the results of the
36 separately picked size fractions (>63 and >125 μm). Although there is indeed additional
37 information on smaller taxa in the 63-125 μm fraction, the overall patterns prove to be
38 robust. This suggests that it is useful to compare assemblage changes (not absolute
39 numbers!) found in our study with those in other studies, even when the size fractions
40 used in the studies are different.

41 In fact, the striking similarities between the >63 μm and >125 μm records from different
42 Tethys-margin sites (e.g. Speijer and Van der Zwaan, 1996; Peryt et al., 2002; Culver,

1 2003; etcetera) further confirms this. Although different size fractions are used, most
2 Tethys-margin sites portray a similar succession of assemblages.

3 We have now stressed this point in our revised manuscript (page 8, line25).

4

5 **[To estimate benthic foraminiferal accumulation rates (BFAR) in on-land sections**
6 **can be somewhat difficult as sample dry bulk density values are difficult to**
7 **measure. In this work average density values derived from literature are used For**
8 **this reason, I advise caution with the use of these BFAR data to reconstruct export**
9 **productivity changes, and I recommend BFAR is not used as a key parameter to**
10 **interpret benthic foraminiferal faunal changes.]**

11 --

12 We agree with the reviewer that estimating the BFAR in on-land sections can be difficult
13 as sample dry bulk density values are difficult to measure. However, in our study the
14 influence of variations in dry bulk density between different stratigraphic intervals on
15 the estimated BFAR will be minor, as the densities of mudstones, siltstones and
16 claystones generally all fall within a range of 2-2.5 g/cm³ (e.g. Manger et al., 1963). In
17 the Okçular section, the BFAR shows a decrease of more than an order of magnitude.
18 This is such a large decrease, that the influence of any minor variations in dry bulk
19 density will be negligible.

20 Nevertheless, to exclude the possible influence of the (small) differences in dry bulk
21 density, we have now reflected the uncertainty in BFAR, resulting from the uncertainty
22 in dry bulk densities, in our Figure 5, indicated by the a range of accumulation rates
23 possible with bulk densities ranging from 2 to 2.5 g/cm³.

24

25 **[Besides, they calculated BFAR using the number of benthic foraminifera/gr**
26 **sediment for the >63 um size fraction while their assemblage counts have been**
27 **done in the >125 um size fraction. This must be changed for consistency as faunal**
28 **patterns in these two size fractions can be quite different.]**

29 --

30 As indicated above, the choice to use the >125 um size fraction to assess changes in the
31 benthic foraminiferal assemblages was a practical one: in this size fraction most
32 specimens could be identified up to species level, allowing for the most accurate
33 assessment of the benthic foraminiferal assemblage. We agree that any analyses or
34 measurement pertaining to diversity and changes in relative abundances should be
35 performed on the >125 um size fraction for consistency.

36 However, in this study, we apply the benthic foraminiferal accumulation rate as an
37 independent, semi-quantitative proxy for productivity and/or food supply to the sea

1 floor (cf. Jorissen et al., 2007 and references therein). This general concept is based on
2 the idea that as more food is available to the benthic community, there is more
3 ecological 'space' and, hence, more foraminifera can live on the sea floor. This does not
4 apply to a specific size fraction, but to all foraminifera living on the sea floor.

5 Therefore, in our opinion, for a proper assessment of the 'ecological state' of the benthic
6 community, one should include all foraminifera, not just a specific subset.

7 To concede to the reviewer, we have now provided both the >63 um size fraction BFAR
8 and the >125 um size fraction BFAR in our Data Set S2 (supplementary materials).

9

10 **[Benthic foraminiferal counts have been made by counting 300 specimens for**
11 **each samples. This is a standard counting threshold widely used in benthic**
12 **foraminiferal quantitative studies. However in this specific case I encourage the**
13 **use of species-specimens plots to establish the most suitable number of specimens**
14 **to count (see Thomas, 1990). The use of species-specimens plots allows to ensure**
15 **that species diversity is well represented. In an outer-neritic upper bathyal site**
16 **species diversity might be higher than in the deep sea settings, where the**
17 **standard average of 300 specimens is usually employed. Since the relevance of**
18 **diversity changes among benthic foraminifera for this study I would perform a**
19 **species-specimen plot for each of the 4 intervals recognized in order to assure**
20 **species diversity is well represented.]**

21 --

22 The reviewer argues that the number of specimens per sample may be too low to
23 capture the full diversity, since in an outer neritic-upper bathyal site diversity may be
24 higher than in the deep-sea. First of all, we note that a selection of >250 specimens per
25 sample is a standard procedure, both in deep-sea and continental margin studies (e.g.
26 Murray, 2006). Some authors recommend a higher number, e.g. counts of 300-400
27 specimens (Lowe and Walker, 1997). In this study, only in two cases a slightly lower
28 sum than 300 was obtained (245 and 269 specimens, respectively). In all other cases,
29 the sum was well over 300, and often over 500 (Figure 4 in the manuscript).

30 In other studies on deep-sea and outer neritic benthic foraminifera across the K-Pg
31 boundary, for instance the study from the Bidart section (Alegret et al., 2004), the Walvis
32 Ridge section (Alegret et al., 2007), the Agost section (Alegret et al., 2003), and the El Kef
33 section (Speijer and van der Zwaan, 1996), the counted number of specimens is mostly
34 200-300. Compared to these studies, the Fisher alpha (which calculated from number of
35 taxa and total specimen count per sample) and Shannon H diversity are lower in our
36 study, also in the cases where the counted number of specimens is higher than 600. As
37 Fisher-alpha should in theory not be sensitive to number of specimens counted,
38 especially when a relatively high sum of >250 is reached (see also the charts in Fisher et
39 al., 1943), this is a strong indication that diversity in our study is indeed systematically
40 lower than in the other sites mentioned, instead of higher. Finally, if the number of
41 species encountered in each sample is plotted against the number of specimens counted
42 per sample (SI Fig. S2), we see no trend towards higher numbers of species with

1 increasing sample size. We thus argue that we do not have any indication that the
2 number of specimens in our study may be too low to capture the full diversity.

3 To further clarify this, we have now included an additional section in our Supplementary
4 Information (SI Text S3 and SI Figure S2).

5

6 **[4. Results: please mention in the text (1) the number of samples along with their**
7 **stratigraphic position for each of the recognized intervals (benthic foraminifera);**
8 **(2) thickness and approximate duration of each interval.]**

9 --

10 We are aware of the complications that arise when benthic foraminiferal data, dinocyst
11 data or other assemblage data are plotted in graphs that are completely black, so-called
12 'filled silhouettes'. In such graphs, it is impossible to determine the sample depths from
13 the graph and to determine the number of samples used to create the graph. For this
14 reason, we decided to use colored silhouettes with horizontal black lines at each sample
15 depth. This way, it becomes clear immediately how many samples were studied in each
16 interval, and at which depths these samples were taken. Adding numerical data on the
17 number of samples studied and their stratigraphic position in the figures is therefore, in
18 our opinion, unnecessary. However, if the reader would be interested in exact sample
19 depths and numbers of samples used, they are referred to the SI where all information is
20 outlined in detail.

21 We have now indicated the recognized intervals in our Data Sets S1 and S2, so that it
22 becomes clear which samples belong to which interval. It should be noted that both the
23 stratigraphic depth and biostratigraphic tie-points are indicated in the figures. This
24 allows the reader to address both the thickness and approximate durations of each
25 interval.

26

27 **[5. Discussion: -Paragraph 5.1: As highlighted by the review paper of Culver**
28 **(2003) and by Thomas (2007) there is no agreement regarding the ecological**
29 **meaning of the generally low-diversity benthic foraminiferal assemblages**
30 **occurring just above the K/Pg boundary. Even though similar changes between**
31 **the % of epifaunal and infaunal species can be recognized between different**
32 **records, such % changes can have different environmental meanings in different**
33 **environmental settings. So I suggest caution in drawing Tethys-wide**
34 **environmental scenarios based on changes in the proportion of epifaunal-infaunal**
35 **species.]**

36 --

37 We agree with the reviewer that changes between the % of epibenthic and endobenthic
38 taxa can have different environmental meanings in different environmental settings.

1 Especially when one compares shelf sites, such as in the Tethys, with deep marine, open
2 ocean sites, such as in the central Pacific, the ecological meaning of, for example, high
3 abundances of endobenthic taxa can be different. However, particularly for this reason,
4 we mainly compare sites in the Tethys ocean, characterized by similar palaeodepths
5 (upper bathyal/outer neritic), similar palaeolatitudes (25-35°) and similar
6 sedimentologies (mixed carbonate-siliciclastic sedimentation), which, therefore,
7 represent similar environmental settings. We therefore argue that Tethys-margin-wide
8 environmental scenarios *can* be drawn based on the recorded signals in these records.

9

10 **[Paragraph 5.2.1: In this paragraph the authors seem to use the Living Ocean**
11 **model (D'Hondt and Zachos, 1998) to explain their data. In my opinion they**
12 **should first provide a sound interpretation of their dataset and then, argue**
13 **whether their dataset fits (or not) with the main models used to explain the K/Pg**
14 **$\delta^{13}C$ shift.]**

15 --

16 The first paragraph of section 5.2.1 describes our dataset. To address the comment of
17 the reviewer, we have now also included a couple of sentences to provide an
18 interpretation of our dataset, independent of the Living Ocean model. The argument
19 whether these data fit the main model, now follows in the next section.

20

21 **[Further, which new contributions brings their own data to a further**
22 **development/understanding of these models? In my opinion this is an aspect**
23 **which is currently not sufficiently addressed in the paper.]**

24 --

25 We do not fully understand this comment of the reviewer. In section 5.2.2, we describe
26 what new insights our study brings, showing that, as a result of the reduced biological
27 pump efficiency, more nutrients became available for the earliest Paleocene
28 phytoplankton community. Our study is the first to suggest that at Tethyan neritic to
29 upper bathyal sites this increased nutrient availability is reflected by the higher
30 abundance of hexaperidinioids.

31

32 **[Paragraphs 5.2.2&5.2.3: As for what concern benthic foraminifera, the work cited**
33 **in these paragraphs used different size fractions for their studies (either >63 μm**
34 **or >125 μm) so direct comparisons among datasets are so far not possible.]**

35 --

36 See point 3.

1 Note that in our study, the comparison is drawn between the Okçular and El Kef
2 datasets, both of which are based on the >125 µm fraction. In addition, the study by
3 Ernst et al. (2006) has convincingly shown that, although there are minor differences
4 between >63 µm fraction and >125 µm fraction datasets, the overall biotic patterns
5 prove to be robust. This suggests, in contrast to the reviewer's view, that comparisons
6 between overall assemblage changes between different studies are possible, even when
7 different size fractions are used.

8 The striking similarities between the >63µm and >125µm records from different
9 localities (e.g. Speijer and Van der Zwaan, 1996; Peryt et al., 2002; Culver, 2003; etcetera)
10 actually confirms this. Although different size fractions are used, most Tethys-margin
11 sites portray a similar succession of assemblages.

12

13 **[6. Conclusion: The conclusion paragraph should be focused on summarizing the**
14 **findings of the paper. Personally I think it should be rewritten highlighting the**
15 **paper's data and their meaning. This is first of all a paper which presents new**
16 **ecological data from a new section spanning the K/Pg boundary, it is not a review**
17 **paper.]**

18 --

19 We differ in opinion with the reviewer on the structure of the conclusion. Over the last
20 decades, numerous studies have been published on K-Pg boundary benthic foraminiferal
21 and dinocyst records, from an array of sites around the world. The most novel, exciting
22 aspect of our study is not that we are adding an extra benthic foraminiferal and dinocyst
23 study to this collection. Rather, it is the combination of our new ecological data with
24 existing records in the same geographical region that provides us valuable new insights
25 in the paleoecological and paleoceanographic consequences of the early Danian 'Living
26 Ocean' condition in this region.

27

28 **[7. Figures 2-6: please add the number of samples studied and their stratigraphic**
29 **position.]**

30 --

31 We used colored silhouettes with horizontal black lines at each sample depth. This way,
32 it becomes clear immediately how many samples were studied in each interval, and at
33 which depths these samples were taken. Adding numerical data on the number of
34 samples studied and their stratigraphic position in the figures is therefore, in our
35 opinion, superfluous. However, if the reader would be interested in exact sample depths
36 and numbers of samples used, they are referred to the SI where all information is
37 outlined in detail.

38

39

1 **[Figure 6: please add the duration of each interval like in the previous figures.]**

2

3 OK. We will include the stratigraphic tie-points in Figure 6, similar to the previous
4 figures.

5

6

7 **[Minor remarks: Abstract: Pag. 1-L26: beginning of the line, please insert “in” after
8 comma.]**

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10 OK

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12 **[Text: Pag. 2-L13: “toward” repeated twice.]**

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14 Corrected

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16 **[Pag. 4-L11: “records” repeated twice.]**

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18 Corrected

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20 **[Pag. 5-L22: please delete “refractory”.]**

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22 OK

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Ecological response to collapse of the biological pump following the mass extinction at the Cretaceous-Paleogene boundary

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Abstract. It is ~~by now unequivocally shown~~ commonly accepted that the mass extinction associated with the Cretaceous-Paleogene (K-Pg) boundary (~66 Ma) is related to the environmental effects of a large extraterrestrial impact. The biological and oceanographic consequences of the mass extinction are, however, still poorly understood. According to the Living Ocean model of D'Hondt et al. (1998), the biological crisis at the K-Pg boundary resulted in a reduction of export productivity in the earliest Paleocene. Here, we combine organic-walled dinoflagellate cyst (dinocyst) and benthic foraminiferal analyses to provide crucial new insight into changes in the coupling of pelagic and benthic ecosystems. To this end, we perform dinocyst and benthic foraminiferal analyses on the recently discovered Tethyan K-Pg boundary section at Okçular, Northwestern Turkey and compare the results with other K-Pg boundary sites in the Tethys. The post-impact dominance of epibenthic taxa and an increase of inferred heterotrophic dinocysts in the earliest Paleocene at Okçular are consistent with published records from other Tethyan sites. Together, these Tethyan records indicate that during the early Paleocene more nutrients were available for the Tethyan planktonic community, whereas benthic communities were deprived of food. Hence, in the post-impact phase the reduction of export productivity likely resulted in enhanced recycling of nutrients in the upper part of the water column, all along the Tethyan shelves.

30

1 Introduction

It is now commonly accepted that the Cretaceous-Paleogene (K-Pg) boundary (~66 Ma) mass-extinction was associated with the impact of a large extra-terrestrial body at Chicxulub, Yucatan, Mexico. The short- and long-term environmental implications of this impact resulted in the extinction of a large number of biological clades (Sepkoski, 1996). Based on the fossilized remains, paleontological records suggest that approximately 50% of marine genera became extinct across the K-Pg boundary. This episode thus represents one of the largest mass-extinction events in Earth history (Sepkoski, 1996; D'Hondt, 2005). Apart from short-term global environmental consequences, such as an initial 'impact winter' phase (Alvarez et al., 1980; Vellekoop et al., 2014; Vellekoop et al., *in press*), the event also had major long-term biological consequences. The large-scale extinctions amongst primary producers caused a major restructuring of global food webs and global carbon cycling (D'Hondt, 2005; Coxall et al., 2006). Moreover, a collapse in the oceanic stable carbon isotope gradient between surface and bottom waters persisted for up to a few million years (Hsu and McKenzie, 1985; Zachos et al., 1989; D'Hondt et al., 1998). Initially, the Strangelove Ocean hypothesis was invoked to explain this collapse, suggesting that primary productivity sharply decreased or ceased immediately after the K-Pg boundary, as a consequence of the extinction of primary producers (e.g. Hsu and McKenzie, 1985).

15 However, modelling the carbon isotope gradient response to the extinctions suggests that productivity-carbon burial had to continue nearly unabated to prevent the carbon isotopic signature of the global oceans from drifting ~~toward~~-towards that of the weathering input (Kump, 1991). In addition, both the persistency-persistence of surviving biological groups of primary producers, e.g. dinoflagellates (e.g., Brinkhuis and Zachariasse, 1988), as well as the survival of benthic foraminifera (e.g., Culver, 2003), argue against prolonged cessation of primary productivity in the global oceans. Integration of neritic and deep-sea planktic and benthic foraminiferal carbon isotopic records suggests that the breakdown of this gradient reflects a global collapse of export productivity, i.e., the fraction of organic carbon that sinks from the photic zone to the deep ocean via the biological pump (Kump, 1991; D'Hondt et al., 1998; D'Hondt, 2005; Hilting et al., 2008; Hain et al., 2014; Esmeray-Senlet et al., 2015), rather than the shutdown of primary productivity. This conceptual model is generally referred to as the "Living Ocean" model (D'Hondt and Zachos, 1998; D'Hondt et al., 1998; D'Hondt, 2005). According to the Living Ocean model, total biological productivity recovered rapidly after the extinction event, but the total global export productivity from the photic zone ~~to~~-was reduced for hundreds of thousands of years (D'Hondt et al., 1998; D'Hondt, 2005; Birch et al., 2016). Although there has been a considerable debate on this possible a collapse of the biological pump following the K-Pg boundary mass extinction (e.g. Alegret and Thomas, 2009; Hull et al., 2011), most recent studies are in agreement that global, post-K-Pg export productivity was reduced to some extent (e.g. Esmeray-Senlet et al., 2015; Birch et al., 2016). Current discussions mostly are related to the severity of the reduction of export productivity or on the geographical differences (i.e. the 'heterogeneity') of the oceans. In particular the records from the Pacific open ocean could, potentially, be explained as showing no reduction of the biological pump (e.g. Alegret et al., 2012; Hull et al., 2011), while sites from the Tethys Ocean, Atlantic

Ocean, Southern Ocean and Indian Ocean show convincing evidence for a collapse of a biological pump at the K-Pg boundary (e.g. following Thomas, 1990; Olsson et al., 1996; Hull et al., 2011; Alegret et al., 2012).

5 ___The inferred reduction in the organic flux to deep waters recorded at most sites might be a consequence of the ecosystem reorganization that resulted from the mass extinction. Variations in species assemblages of pelagic communities can lead to large changes in the rates of particulate export (e.g., Buesseler, 1998; Stemann and Boss, 2012). A general reduction of the number of pelagic grazers (such as macrozooplankton) or a shift in dominance from grazers that create fecal pellets (e.g., fish) to grazers that do not produce fecal pellets, could have greatly reduced the packaging of biomass into large particles that sank to the deep ocean (D'Hondt et al., 1998; D'Hondt, 2005). Grazers that do not produce fecal pellets include, amongst others, heterotrophic dinoflagellates. The record at Gubbio, Italy, indicates that for example in the Tethys Ocean, fish abundances fell abruptly at the K-Pg boundary, remaining depressed for millions of years (Sibert et al., 2014).

10 Additionally, the replacement of large Cretaceous planktic foraminiferal and calcareous nannoplankton tests by smaller early Paleocene forms (e.g., Bernaola and Monechi, 2007; Molina, 2015) might have reduced biomineral ballasting (Armstrong et al., 2002) in the earliest Paleocene, resulting in a further reduction of the carbon flux to the ocean floor (Coxall et al., 2006).

15 Although numerous studies have been performed to seek evidence for the K-Pg boundary impact, the millennial-scale biotic responses to this large-scale paleoceanographic change are still poorly documented and not fully understood. Some of the most intensely studied microfossil groups used in paleoenvironmental reconstructions, such as planktonic foraminifera and calcareous nannoplankton, experienced major extinctions and subsequent radiations (e.g., Smit, 1982; Huber et al., 2002; Coxall et al., 2006; Molina, 2015; Schueth et al., 2015), hampering environmental reconstructions across the K-Pg boundary interval. In contrast, benthic foraminifera and organic-cyst producing dinoflagellates are much better suited, as they show no significant extinction above background levels at the end of the Cretaceous (Brinkhuis and Zachariasse, 1988; Culver, 2003).

20 A few high-resolution K-Pg boundary benthic foraminiferal and organic-walled dinoflagellate cysts (dinocyst) records have been published, particularly from the southern and western shallow margins of the Tethys Ocean, for example from Tunisia, Israel, Egypt, Spain and Morocco (Brinkhuis and Zachariasse, 1988; Eshet et al., 1992; Keller et al., 1992; Coccioni and Galeotti, 1994; Speijer and Van der Zwaan, 1996; Brinkhuis et al., 1998; Peryt et al., 2002; Alegret et al., 2003; Slimani et al., 2010; Vellekoop et al., 2015) (Figure 1). These records thus potentially provide a comprehensive, Tethyan ocean-wide portrayal of the changes in pelagic-benthic coupling across the K-Pg boundary. The benthic foraminiferal and dinocyst records from the southern margin of the Tethys do reveal indications for major, short-term oceanographic ~~changes, including~~ changes in, for example, temperature, redox and trophic conditions across the K-Pg boundary (e.g., Brinkhuis and Zachariasse, 1988; Speijer and Van der Zwaan, 1996; Brinkhuis et al., 1998). Especially quantitative benthic foraminiferal records show a strong response to the impact, generally portraying an abrupt benthic community impoverishment across the boundary. At many of these K-Pg boundary sites, after a short-lived proliferation of endobenthic forms (e.g., Coccioni and Galeotti, 1994; Alegret et al., 2015), epibenthic forms dominate the initial post-impact 'disaster' phase (Culver, 2003). Since in general endobenthic forms are considered indicative for a high flux of organic matter to the seafloor and/or relatively low oxygen conditions, and epibenthic forms indicate more oligotrophic environments (e.g., Corliss, 1985; Peryt et al., 2002; Jorissen et al., 2007;

Woelders and Speijer, 2015), the post-impact abundance of epibenthic forms is often explained as food starvation at the sea floor (Culver, 2003). Following this ‘disaster’ phase, most benthic foraminiferal records show a relatively long recovery phase, with endobenthic forms slowly returning as diversity starts to increase again (Alegret et al., 2003; Culver, 2003), as endobenthic microhabitats supposedly diversified (Speijer and Van der Zwaan, 1996).

5 Although combining quantitative dinocyst and benthic foraminifera analyses could provide crucial insight into changes in pelagic-benthic coupling (e.g., Guasti et al., 2005), perhaps surprisingly, no such attempts have been made for the K-Pg boundary interval so far. Earlier studies discussed either benthic foraminiferal *or* dinoflagellate response to the K-Pg boundary, each without making an attempt to combine the results of these studies into a comprehensive, integrated ocean-wide explanation for ecological patterns observed across the boundary. In addition, although the southern margins of the Western
10 Tethys provide a fair number of high-resolution records spanning the K-Pg boundary, no such high resolution records yet exist from the northeastern margins of the Western Tethys. To be able to provide a comprehensive, Tethys ocean-wide portrayal of the surface and bottom water ecological changes across the K-Pg boundary and the coupling between pelagic and benthic systems, additional dinocyst and benthic foraminiferal records need to be generated from the northeastern margin of the Tethys.

The Mudurnu-Göynük Basin in the Central Sakarya Region, Turkey, provides new opportunities for high-resolution K-Pg
15 boundary benthic foraminiferal and dinocyst records from the northern margin of the Tethys. Recently, well-preserved outcrops of ancient continental margin deposits spanning the K-Pg boundary have been discovered in this basin (Açikalin et al., 2015). These outcrops include, amongst others, the Okçular section. Here, an integration of dinocyst and benthic foraminifera records of this biostratigraphically well-constrained K-Pg boundary transition is used to provide new insights in changes in, and the relationship between, planktic and benthic communities.

20 ~~By~~ Linking these records to both the previously generated bulk-carbonate carbon isotope record of this section (Açikalin et al., 2015) and to other benthic foraminiferal and palynological records ~~records in the Tethys ocean enables a Tethys-margin wide portrayal of the K-Pg boundary pelagic crisis and the biological changes caused by the collapse of export productivity the biological changes recorded will be placed in the context of the K-Pg boundary pelagic crisis and collapse of export productivity in the Tethys ocean.~~ This integrated approach enables an evaluation of the paleoecological and paleoceanographic
25 consequences of the early Danian ‘Living Ocean’ condition.

2 Geological setting and age assessment

The Okçular section is located in the Mudurnu-Göynük Basin (Northwestern Turkey; Figure 1). In this basin, the K-Pg boundary interval is represented by the Tarakli Formation (Saner, 1980; Altiner, 1991; Açikalin et al., 2015). In the eastern side of the basin, the upper Maastrichtian is characterized by an intercalation of mudstones and turbidites, whereas in the
30 western side of the basin the turbidites are absent. The K-Pg boundary is marked by a reddish ejecta layer at the base of a 15-20 cm thick boundary clay layer. Throughout the basin, the lower 30-50 m of the Danian is characterized by a rhythmic alternation of fine-grained limestones and carbonate-rich mudstones (Açikalin et al., 2015). During the latest Cretaceous to

earliest Paleocene this site was characterized by mixed siliciclastic-carbonate sedimentation in an outer neritic to upper bathyal environment (Açikalin et al., 2015).

The Okçular section has been analyzed for siderophile trace elements, including Ir and other platinum group elements (PGEs), bulk stable carbon isotopes, planktic foraminifera, calcareous nannofossils and dinocysts. Based on these results, a detailed biostratigraphy was defined (Açikalin et al., 2015), allowing a confident age assessment of the boundary interval. The age model shows that the section contains a chronostratigraphically complete K-Pg boundary interval. The studied interval ranges from the top part of the Maastrichtian *A. mayaroensis* Zone up to the basal part of the Danian planktic foraminiferal Zone P1b and covers globally occurring First Occurrences (FO) of dinocyst marker taxa such as *Senoniasphaera inornata*, *Damassadinium californicum* and *Carpatela cornuta*.

10

3 Materials and methods

3.1 Sampling

High-resolution (cm-scale) sample sets were used that were acquired during 2 field campaigns, in 2010 and in 2011. For more detail on these sampling campaigns, see Açikalin et al. (2015). The samples were split for micropaleontological and palynological analyses.

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3.2 Foraminiferal analysis

Twenty-seven samples were processed at KU Leuven for foraminiferal studies following standard micropaleontological procedures. Of these samples, 20 samples were used for quantitative benthic foraminiferal analyses (Fig. 2). Rock samples were dried in an oven at 60°C for at least 24 hours. Depending on sample size, 4 to 60 grams of dry rock were soaked in a soda solution (50g/l Na₂SO₄). After disintegration, samples were washed over 2 mm and 63-µm sieves. If necessary, the tenside Rewoquat was used to clean the residues and the procedure was repeated. Clean residues were dry-sieved into three fractions: 63-125 µm, 125-630 µm and >630 µm. Representative aliquots of the >125 µm fraction were obtained, containing at least 300 benthic foraminiferal specimens. Picked specimens from this size fraction were permanently stored in Plummer slides. Benthic foraminifera were identified using the taxonomy of Cushman (1946), Cushman (1951), Kellough (1965), Aubert and Berggren (1976), Berggren and Aubert (1975) and Speijer (1994).

25

Benthic foraminifera are commonly used as indicators for bottom water oxygenation and trophic conditions (e.g., Jorissen et al., 2007). Here, the Benthic Foraminiferal Accumulation Rate (BFAR, number of foraminifera per cm² per kyr; see Text S2 in the supporting information for details on the estimation of the BFAR) was calculated as a semi-~~qualitative~~-quantitative proxy for paleoproductivity (Jorissen et al., 2007 and references therein). In addition, the percentage of endobenthic morphotypes was calculated using the assumed microhabitat preferences inferred from benthic foraminiferal morphotype analysis (e.g., Corliss, 1985; Corliss and Chen, 1988; Alegret et al., 2003; Woelders and Speijer, 2015). In general, endobenthic

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forms are considered indicative ~~for-of~~ a high flux of ~~refractory~~ organic matter to the seafloor and/or relatively low oxygen conditions, while abundance of epibenthic forms is considered characteristic for more oligotrophic environments (Jorissen et al., 1995; Peryt, 2004; Jorissen et al., 2007). Furthermore, the bi- and triserial endobenthic forms are particularly indicative for high food supply and low oxygenation (e.g., Bernhard, 1986; Corliss and Chen, 1988; Jorissen et al., 2007). Therefore, in this study, the percentage of endobenthic forms was calculated for each sample, as well as the percentage bi-/triserial benthic taxa, to unravel food supply and oxygenation patterns.

It should be noted that assuming such an analogue with modern fauna has limitations and shortcomings. For instance, calculating the percentage endobenthics based on morphotypes and using bi-/triserials as an indicator for hypoxia and high food supply can have exceptions (Buzas et al., 1993; Jorissen et al., 2007 and references therein).

3.3 Palynological analysis

In this study, the palynological data from Açıkalın et al. (2015) ~~was-were~~ analyzed and interpreted. In addition, two additional samples were analyzed (OK 1.5 and OK 6) to increase the resolution of the dataset, and two samples of the Açıkalın et al. (2015) dataset were re-counted (OK 2.5 and OK 250; see Supplementary Information Data Set 2). Quantitative slides of the 15-250 μm fraction were used. All slides are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, The Netherlands.

To identify major changes in the dinocyst record, morphologically closely related taxa were grouped into complexes using a similar approach to Schiøler et al. (1997); Sluijs and Brinkhuis (2009) and Machalski et al. (2016). In our study, the following morphological complexes were established: (1) the *Spiniferites* complex, combining all species of *Spiniferites* and the morphologically similar genus *Achomopshaera*; (2) *Manumiella* spp., grouping all species of *Manumiella*; (3) hexaperidinioids, lumping all other peridinioid cysts with a hexaform archeopyle; (4) other dinocysts, which includes all other dinocyst taxa and unidentifiable dinocysts (Fig. 3).

Of these different dinocyst groups, previous studies have shown that in the Tethys in particular the hexaperidinioids show strong variations across the K-Pg boundary (Brinkhuis et al., 1998; Vellekoop et al., 2015). Based on statistical correlations between palynological records and other paleo-proxies, it has been suggested that this inferred heterotrophic group flourished best under high-nutrient conditions in the photic zone (Eshet et al., 1994; Brinkhuis et al., 1998; Sluijs and Brinkhuis, 2009). Therefore, in this study, abundances of hexaperidinioids are considered indicative of nutrient availability in the photic zone (see Fig. S1 and Text S1 in the supporting information for a more detailed discussion on this matter).

3.4 Statistical analysis

To assess changes in diversity of benthic foraminifera and dinocysts across the studied interval, the Shannon diversity index (H), the species richness per sample (S), number of specimens observed per sample (N) and the Berger-Parker index were calculated for both biological groups, following Hayek and Buzas (2013) (Fig. 4). In addition, to recognize the main faunal

associations within the benthic foraminiferal data, a cluster analysis was performed, using Paired Group (UPGMA) correlation distance.

Q-mode Non Metric – Multi Dimensional Scaling (NM-MDS) was performed on the benthic foraminiferal sample compositions to assess patterns in assemblage response to K-Pg boundary perturbations. Since taxa may not have a linear response to environmental changes across the K-Pg boundary, Q-mode NM-MDS is preferred over PCA and CCA (Ramette, 2007).

4. Results

4.1 Benthic Foraminifera

The benthic foraminiferal record of the Okçular section is characterized by a major turnover across the K-Pg boundary (Figs. 2,4,5,6). Of the common taxa, 8 out of 30 (~27%) disappear across the K-Pg boundary. After the K-Pg boundary crisis, 3 new taxa appear. The estimated BFAR shows a major decrease across the boundary (Fig. 5). For the foraminiferal counts and illustrations of common forms, see Dataset S1 and Figs. S2, S3.

The cluster analysis allows the identification of 4 main clusters of benthic foraminiferal taxa, Clusters A to D (Fig. 2). Cluster C is relatively large and can be subdivided into 5 sub-clusters. Based on the succession of benthic faunal assemblages, characterized by strong changes in the Shannon diversity index (H), 4 intervals can be recognized in the benthic foraminiferal record of the Okçular section (Figs. 4, 6).

The first interval comprises the uppermost Maastrichtian and is characterized by a relatively high diversity, dominated by taxa of Cluster D. In this assemblage, the bi-/triseriate benthic taxa are relatively abundant (22-28%), with characteristic taxa such as *Bulimina arkadelphia*, *Eouvigerina subsculptura* and *Praebulimina reussi*. About 50-60% of the assemblage consists of inferred endobenthic taxa. The K-Pg boundary marks an abrupt benthic community impoverishment and the decimation of taxa of Cluster D. Above the boundary, the bi-/triseriate benthic taxa virtually disappear from the record (mostly below <0.5%).

The second interval, characterized by low diversity, comprises the lowermost Danian, approximately correlative to planktic foraminiferal Zone P0. In this interval epibenthic forms are most abundant (70-90%). It is dominated by taxa of Cluster A, encompassing successive peak occurrences of the taxa *Anomalinoides praeacutus*, *Trochammina* spp. and *Cibicidoides pseudoacutus*.

The third interval covers the part of the succession approximately correlative to planktic foraminiferal Zone P α . This interval is characterized by a recovery of diversity, although the diversity is still lower than that of the top Maastrichtian assemblage. The abundance of taxa of Cluster A slowly decreases and taxa of Cluster B, mainly represented by *Osangularia plummerae* and *Cibicidoides* sp., become abundant. Endobenthic forms recover and make up 30-40% of the total assemblage.

The fourth interval starts in the interval correlative to Zone P1a. Here, the benthic community has recovered as the diversity has stabilized and is almost similar to pre-impact values. This interval is characterized by taxa of Cluster C, a typical Paleocene

Midway-type fauna (Berggren and Aubert, 1975), with representatives such as *Anomalinoidea praeacutus*, *Coryphostoma midwayensis*, *Cibicidoides alleni* and *Osangularia plummerae*.

4.2 Palynology

5 Palynological samples from the Okçular site yield an abundance of palynomorphs, dominated by dinocysts and with minor contributions of acritarchs, prasinophytes, organic foraminiferal linings and terrestrial palynomorphs (Dataset S2). The dinocyst associations of the Mudurnu-Göynük Basin are relatively diverse, including components characteristic for both the Tethyan and Boreal realms (Açikalın et al., 2015). As expected, the dinocyst record does not show major changes in diversity across the K-Pg boundary (Fig. 4). There is a steady decrease in dinocyst diversity from planktic foraminiferal Zone P1a
10 upwards, but this is probably a long-term change not related to the impact. Also the estimated Dinocyst Accumulation Rate (DAR, number of preserved cysts per cm² per kyr; see Text S2 in the supporting information for details on the estimation of the DAR) shows no major changes across the K-Pg boundary.

Throughout the palynological record, the *Spiniferites* complex is consistently the most dominant morphogroup, in general comprising 40-50% of the total assemblage (Fig. 3). Similar to other K-Pg boundary sites worldwide (Habib and Saeedi, 2007),
15 *Manumiella* spp. shows an episode of higher relative abundances near the top of the Maastrichtian, some 30-40 cm below the K-Pg boundary. Hexaperidinioids generally make up a relatively small component of the Maastrichtian assemblage (3-17%), but show a strong increase across the K-Pg boundary. In the boundary clay layer, correlative to planktic foraminiferal Zone P0, this group increases up to 35% of the assemblage. In the peak intervals, the hexaperidinioids are mostly represented by representatives of the genera *Senegalinium* and *Cerodinium*. After an initial drop in relative abundance in the upper half of
20 Zone P0, this group reaches a second maximum (~35%) at the base of Zone Pa and remain relatively abundant (15-30%) up to Zone P1a. After this, the hexaperidinioids slowly decrease to the top of the studied interval. The ‘other dinocysts’ group, with representatives such as *Areoligera* spp., *Impagidinium* spp., *Hystrichosphaeridium tubiferum*, *Operculodinium centrocarpum* and *Palynodinium grallator*, generally makes up 25-50% of the assemblage.

25 5. Discussion

5.1 Tethyan benthic foraminiferal turnover sequence

The major turnover in the benthic community at Okçular is largely comparable with earlier published benthic foraminiferal records from the margins of the Tethys (Speijer and Van der Zwaan, 1996; Alegret et al., 2003; Culver, 2003 and references therein). Although both the size fractions used (>63µm vs >125µm) and specific taxa making up the foraminiferal assemblages,
30 differ per site, other Tethyan K-Pg boundary sites with faunas from middle neritic to upper bathyal depths generally portray a similar succession of assemblages (Speijer and Van der Zwaan, 1996; Peryt et al., 2002; Culver, 2003), involving the successive occurrences of (1) a typical high diversity assemblage in the Maastrichtian; (2) a low diversity ‘disaster’ assemblage directly after the K-Pg boundary impact, characterized by a short-lived bloom of endobenthic taxa observed in several high-resolution records (e.g., Coccioni and Galeotti, 1994; Speijer and Van der Zwaan, 1996), followed by a dominance of

epibenthic taxa; (3) a 'recovery' assemblage, characterized by an increasing diversity and returning endobenthic forms; and (4) a new, high diversity assemblage, dominated by a Paleocene, Midway-type fauna, with both epi- and endobenthic forms present.

Hence, based on this succession of benthic faunal assemblages, which are characterized by strong changes in diversity (H), the K-Pg boundary benthic foraminiferal records from the Tethys can be subdivided in four intervals (Figs. 2,4-6). These intervals I to IV approximately correspond to the uppermost Maastrichtian, planktic foraminiferal Zone P0, Zone P α -P1a and Zone P1a-P1b, respectively, and therefore, this succession roughly follows the 5-fold sequence of Smit and Romein (1985).

The transition in benthic foraminiferal assemblages in the Tethys is also illustrated by Q-mode NM-MDS (Fig. 7). The Q-mode NM-MDS of the benthic foraminiferal sample compositions of Okçular (this study) and El Kef (Speijer and Van der Zwaan, 1996), combined in one analysis, demonstrates that although the assemblages differ between these localities, the responses of the benthic foraminiferal assemblages to the K-Pg boundary perturbations express similar patterns across the K-Pg boundary. At both Okçular and El Kef, the benthic foraminiferal records show a rapid transition from a stable Maastrichtian assemblage to an earliest Danian disaster phase in Zone P0, followed by a gradual change back towards conditions similar to the Maastrichtian. Therefore, both the succession of benthic faunal assemblages, including diversity-indices, as well as Q-mode NM-MDS analysis provide powerful tools to allow comparison of K-Pg boundary benthic foraminiferal records from different localities.

5.2 Ecological responses to reduced export productivity

5.2.1 Okçular section

The palynological, benthic foraminiferal and bulk stable isotope records of the Okçular section show major changes across the K-Pg boundary interval (Figs. 2-7), portraying the biological crisis following the impact (D'Hondt, 2005; Esmeray-Senlet et al., 2015). Following the K-Pg boundary mass extinction, endobenthic taxa, including bi-/triseriate benthic taxa, almost disappear from the benthic community and the estimated BFAR shows a major decrease (Fig. 5). This interval, approximately correlative to foraminiferal Zone P0, represents the 'disaster' phase. The dramatic drop in bi-/triseriate benthic taxa (Fig. 6) and major decrease in BFAR (Fig. 5) indicate that there was a coinciding drop in food supply to the benthic community, indicating that the transport of organic matter to the sea floor must have also decreased. In the dinocyst community on the other hand, hexaperidinioids show a strong increase in relative abundance during this phase (Figs. 3, 6, 7), suggesting an increase in nutrient availability in the photic zone, while the DAR remains relatively stable across the K-Pg boundary (Fig. 5).

~~These observed changes in the benthic foraminiferal and dinocyst communities in the Okçular record are likely caused by the major reduction of both the efficiency and strength of the biological pump, in accordance with the 'Living Ocean' model (D'Hondt and Zachos, 1998; D'Hondt et al., 1998; D'Hondt, 2005; Coxall et al., 2006). As bulk carbonate $\delta^{13}\text{C}$ reflects the isotopic composition of the surface ocean, which is set by burial fractions and by the photosynthetic isotope effect (Kump, 1991; Hain et al., 2014), the excursion recorded in bulk $\delta^{13}\text{C}$ records worldwide and the rapid collapse in surface to deep ocean carbon isotope gradients likely reflect the reduction of the global intensity (i.e. efficiency) of the biological pump (Hain et al.,~~

~~2014). The dramatic drop in bi-/triseriate benthic taxa (Fig. 6) and major decrease in BFAR (Fig. 5) indicate that there was a coinciding drop in food supply to the benthic community, indicating that the transport of organic matter to the sea floor must have also decreased.~~

The decrease in benthic diversity and the blooms of opportunistic *Trochammina* spp. and *Cibicidoides pseudoacutus* suggest that the benthic community experiences additional stress during Zone P0, besides food limitation (conform Jorissen et al., 2007). This stress might include reduced oxygen levels, as was suggested for instance by Speijer and van der Zwaan (1996) who identified epibenthic *Cibicidoides pseudoacutus* as a potentially hypoxia-resistant taxon. As a collapse of the biological pump should lead to enhanced remineralization of organic matter in the photic zone, it is indeed likely that the oxygen minimum zones expanded and shoaled, leading to oxygen stress on the sea floor. However, no unequivocal evidence for this ecological preference of *C. pseudoacutus* was provided. Furthermore, as there is no other evidence from the investigated Okçular record pointing towards hypoxic conditions during this interval, the cause for the potential additional stress for the benthic foraminiferal community during Zone P0 remains uncertain. Organic-walled cyst producing dinoflagellates did not suffer extinctions and may have become a more important component in the earliest Paleocene phytoplankton community. Hence, besides the reduction of the amount of organic matter transported to the sea floor, the composition of food supplied by the photic zone likely changed significantly across the K-Pg boundary as well (D'Hondt, 2005), possibly presenting an additional stress factor for the benthic community (Alegret and Thomas, 2009).

5.2.2 Tethys Ocean

The patterns in benthic foraminiferal and dinoflagellate response to the K-Pg boundary perturbations at Okçular appear to be characteristic for shelf section in the Tethyan Realm. In Tunisia and Spain, where both benthic foraminiferal and dinoflagellate records are available, the earliest Danian is also characterized by a decrease in endobenthic foraminifera at the sea floor (Speijer and Van der Zwaan, 1996; Peryt et al., 2002; Alegret et al., 2003) and, simultaneously, blooms of hexaperidinioids in the water column (Brinkhuis et al., 1998; Vellekoop et al., 2015; Fig. 8). In the Ouled Haddou section, Morocco, in the westernmost Tethys (Fig. 1), the lowermost Danian is also characterized by a strong increase of the hexaperidinioid *Senegalinium* group, up to 30% of the assemblage (Slimani et al., 2010), very similar to the Okçular record (Fig. 8).

Strikingly similar to the dinocyst record from the Okçular section, the record from El Kef, the Global Stratotype Section and Point (GSSP) of the K-Pg boundary, also shows two distinct peaks in hexaperidinioids, one in Zone P0 and one at the basal part of Zone P α . At El Kef, the initial post-impact dominance of hexaperidinioids is nonetheless less pronounced (Fig. 8). This difference in expression might be related to small differences in paleogeographic and paleoceanographic settings between sites.

Some high resolution benthic K-Pg records in the Tethyan Realm also show a short-lived bloom of endobenthic foraminiferal taxa directly after the K-Pg boundary, sometimes accompanied by other indicators of low oxygen levels (e.g. Coccioni and Galeotti, 1994; Speijer and Van der Zwaan, 1996; Kaiho et al, 1999). This suggests that, at least locally, the sea floor was temporarily characterized by hypoxic conditions directly following the impact. This short-lived de-oxygenation is

possibly related to the mass mortality at the K-Pg boundary, resulting in a large, short-lived flux of food to the sea floor. However, since export productivity was greatly reduced after the K-Pg boundary mass extinction, very little “new” organic matter reached the sea floor after the initial post-impact influx. Hence, after accumulated organic matter was remineralized, the benthic community starved, resulting in a transition to an epibenthic-dominated benthic fauna characteristic for well-oxygenated sea floor, similar to the post-impact fauna of the Okçular record.

The combined dinocyst records suggest that the earliest Paleocene shelves of the Tethys were characterized by an increase in nutrient availability in the photic zone, whereas coeval benthic foraminiferal records indicate a major decrease in nutrient supply to the seafloor. These observed changes in the benthic foraminiferal and dinocyst communities are likely caused by the major reduction of both the efficiency and strength of the biological pump, in accordance with the ‘Living Ocean’ model (D’Hondt and Zachos, 1998; D’Hondt et al., 1998; D’Hondt, 2005; Coxall et al., 2006). As bulk carbonate $\delta^{13}\text{C}$ reflects the isotopic composition of the surface ocean, which is set by burial fractions and by the photosynthetic isotope effect (Kump, 1991; Hain et al., 2014), the excursion recorded in bulk $\delta^{13}\text{C}$ records worldwide and the rapid collapse in surface to deep-ocean carbon isotope gradients likely reflect the reduction of the global intensity (i.e. efficiency) of the biological pump (Hain et al., 2014). ~~Theis~~ recorded inverse change in nutrient availability suggests a causal link. A reduced efficiency of the biological pump and associated decrease of the fraction of biomass transported from the photic zone to the seafloor could have resulted in high rates of nutrient recycling in the upper part of the water column (D’Hondt, 2005). This suggests that the reduction of the biological pump strength, recorded by the benthic foraminiferal record, is a consequence of the decreased efficiency of the biological pump, recorded by the carbon isotope and dinoflagellate cyst records. The strong correlation between the bulk carbon isotope curves and the Shannon diversity index (H) of the benthic foraminiferal records at both Okçular ($R^2=0.73$, $p<0.001$) and El Kef ($R^2=0.74$, $p<0.001$) shows that there is a clear link between the changes in benthic foraminiferal assemblages and the collapse and recovery of biological pump efficiency.

As a result of the reduced biological pump efficiency, more nutrients will have been available for the earliest Paleocene phytoplankton community. At Tethyan neritic to upper bathyal sites this is indicated by the higher abundance of hexaperidinioids. Similarly, blooms of eutrophic survivor taxa of calcareous nannoplankton at open ocean sites have been suggested to be related to the build-up of nutrients in the open ocean photic zone (Schueth et al., 2015). Although the carbon isotope gradients between surface and deep waters indicate the recovery of the biological pump took hundreds of thousands of years (Zachos et al., 1989; Kump, 1991; D’Hondt et al., 1998; Coxall et al., 2006; Birch et al., 2016), our records suggest that the enhanced recycling of nutrient in the Tethys was particularly intense during two phases in the first tens of thousands years after the impact (Fig. 8).

5.2.3 Global responses

The decrease in export productivity following the K-Pg boundary can not only be recognized in the Tethyan Realm, but also outside this region. In for example the Atlantic Ocean, Southern Ocean and the Indian Ocean, a decrease of the biological pump strength after the K-Pg boundary was observed in neritic to abyssal environments (e.g., Thomas, 1990; Olsson et al.,

1996; Hull et al., 2011; Alegret et al., 2012). As an example, the benthic foraminiferal K-Pg boundary record of Blake Nose (ODP Hole 1049C, Northwestern Atlantic; Alegret and Thomas, 2004) shows a pattern that is strikingly similar to the records in the Tethyan realm, with a strong decrease of endobenthics in Zone P0, followed by a gradual recovery across Zones P α and P1a (Fig. 8). The similarities between the patterns in the benthic foraminiferal records of the outer neritic to upper bathyal (200-500 m) sites in the Tethys and those in the benthic foraminiferal record of the middle-lower bathyal (1500-1600 m) Blake Nose record (Alegret and Thomas, 2004) suggests that these benthic foraminiferal records record a global decrease in export productivity following the K-Pg boundary.

However, several open ocean sites, mostly in the Pacific, show an opposite trend, with several lines of evidence suggesting an increased biological pump strength at these sites (e.g., Hull et al., 2011; Alegret et al., 2012). This led Alegret et al. (2012) to conclude that the decrease in biological pump strength after the K-Pg boundary was most likely a regional instead of a global effect, arguing against the Living Ocean hypothesis. Low productivity open ocean sites like the central Pacific are characterized by entirely different ecosystem structures than more eutrophic sites, for example in the Tethyan Realm (e.g. Dortch and Packerd, 1989). Therefore, the consequence of the ecosystem reorganization resulting from the mass extinction was likely also entirely different at the open ocean Pacific (e.g., Sibert et al., 2014). Esmeray-Senlet et al. (2015) proposed the term ‘Heterogeneous Ocean’ for this conceptual model, as an alternative to the ‘Living Ocean’ model. Supposedly, the ‘Heterogeneous Ocean’ was characterized by a strong geographic heterogeneity in the extinction patterns and food supply to the sea floor,

Yet, as the main food source for open ocean, deep sea benthic communities generally consists of refractory organic matter (e.g. Jiao et al, 2010), it remains uncertain whether changes in the intensity of recycling of the generally more labile organic matter in the surface ocean will result in changes in the amount of organic matter that benthic communities receive, as they will likely continue to receive recalcitrant organic matter at barely diminished rates, despite the collapse of the biological pump.

~~However~~In addition, it should be noted that, although the biological pump efficiency is generally relatively high in open ocean realms such as the central Pacific, the biological pump strength, i.e. the amount of organic carbon transported from the surface to the deep, is generally very low at these sites (Honjo et al, 2008; Henson et al. 2011). Small changes in absolute biological pump strength at such a locality could therefore have had a large effect on the local, oligotrophic benthic community (Alegret and Thomas, 2009), but likely represented only a small fraction of the net amount of organic matter globally transported to the deep. Hence, even though local biological pump strength might have increased at some low productivity, deep-sea sites, the large decrease in biological pump strength recorded at many other sites means that the net amount of organic matter globally transported out of the surface ocean was likely still reduced in the post-impact world (Birch et al., 2016). Therefore, we argue that such Pacific records represent exceptions to the general pattern and that, although the global ocean response can be characterized as ‘heterogeneous’, the K-Pg boundary mass extinction still resulted in a reduction of the net, total amount of organic matter globally transported out of the surface ocean, while biological productivity recovered rapidly after the extinction event, in accordance with the Living Ocean hypothesis.

5.3 Long term recovery

Following the ‘disaster’ phase, the hexaperidinioid cysts at Okçular and El Kef decreased in abundance and the abundance of endobenthic benthic forms increased again, as the recovery of the benthic community was initiated. This recovery phase is approximately correlative to Zone P α and the basal part of Zone P1a, which, according to the Paleogene age constraints of Vandenberghe et al. (2012), represents at least 300 kyrs. This duration is in agreement with the estimations provided by Birch et al. (2016). During this phase, the carbon isotope records remain well below pre-impact values and the diversity of the benthic foraminiferal community has not yet fully recovered (Figs. 4-8). This indicates that the rapid and short-lived K-Pg boundary disaster was followed by a relatively long recovery phase, in line with previous estimates of a multimillion-year biological recovery (e.g., Coxall et al., 2006). Whilst the impact-related environmental perturbations were short-lived (Kring, 2007; Vellekoop et al., 2014; Vellekoop et al., 2016), the extinctions amongst important biological groups led to a reduction of the organic flux from the photic zone to deep water, resulting in major long-term biological and paleoceanographic reorganizations. Only with the evolutionary recovery of the pelagic community governing the biological carbon pump, did export productivity start to increase again (e.g., Coxall et al., 2006; Birch et al., 2016).

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6. Conclusions

The marine palynological, benthic foraminiferal and bulk stable isotope records of the Okçular and El Kef sections reveal major changes across the K-Pg boundary interval, portraying the biological crisis at the K-Pg boundary and subsequent recovery in the earliest Paleocene. Based on the succession of benthic faunal assemblages at a number of Tethyan shelf sites, four phases can be recognized across the K-Pg boundary interval: the Maastrichtian or pre-impact phase, a disaster phase, a recovery phase and an early Paleocene phase.

Following the K-Pg boundary impact, some localities show a large, short-lived flux of food to the sea floor, likely related to the mass mortality at the K-Pg boundary. However, since export productivity was greatly reduced after the K-Pg boundary mass extinction, it is likely that, after the initial post-impact influx, very little “new” organic matter reached the sea floor. This reduction of export productivity in the post-extinction disaster phase eventually resulted in a lower food supply to the sea floor. This presented a major stress factor for benthic organisms in the Tethys Ocean. The reduced food supply resulted in an abrupt impoverishment of benthic communities. As the downward transport of nutrients was slowed down, recycling in upper layers increased. As a result, more nutrients became available for the earliest Paleocene phytoplankton community, leading to blooms of dinoflagellates along the Tethyan shelves and blooms of calcareous nannoplankton taxa of in more open ocean sites. Our records show that the enhanced recycling of nutrients in the Tethys was particularly intense in the tens of thousands of years after the impact. Following this, the slow evolutionary recovery of the pelagic community governing the biological carbon pump resulted a gradually increasing export productivity in the hundreds of thousands of years after the impact. Hence, the integration of dinocyst and benthic foraminiferal records across the K-Pg boundary provides crucial new insights in the

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ecological responses to the reduction of export productivity following the mass extinction at the Cretaceous-Paleogene boundary, highlighting the direct ecological consequences of the Living Ocean conditions in the post-impact world.

The Supplement related to this article is available online at XXXXX

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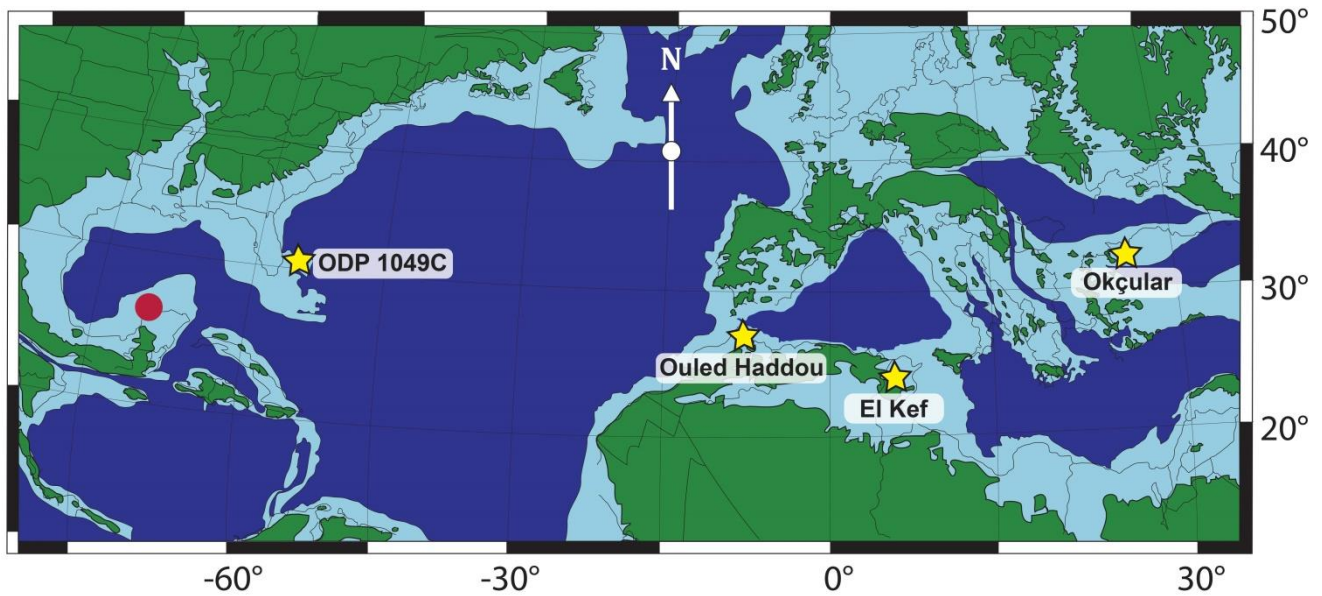


Figure 1: A reconstruction of the late Cretaceous-early Paleogene paleogeography of the North Atlantic and Mediterranean regions, after Scotese (2004) and Scotese and Dreher (2012). The four sites that are discussed are indicated in the figure: Okçular section, Turkey (Açikalin et al., 2015; this study), El Kef, Tunisia (Brinkhuis and Zachariasse, 1988; Speijer and Van der Zwaan, 1996; Brinkhuis et al., 1998), Ouled Haddou, Morocco (Slimani et al., 2010) and ODP 1049C (Blake Nose; Alegret and Thomas, 2004).

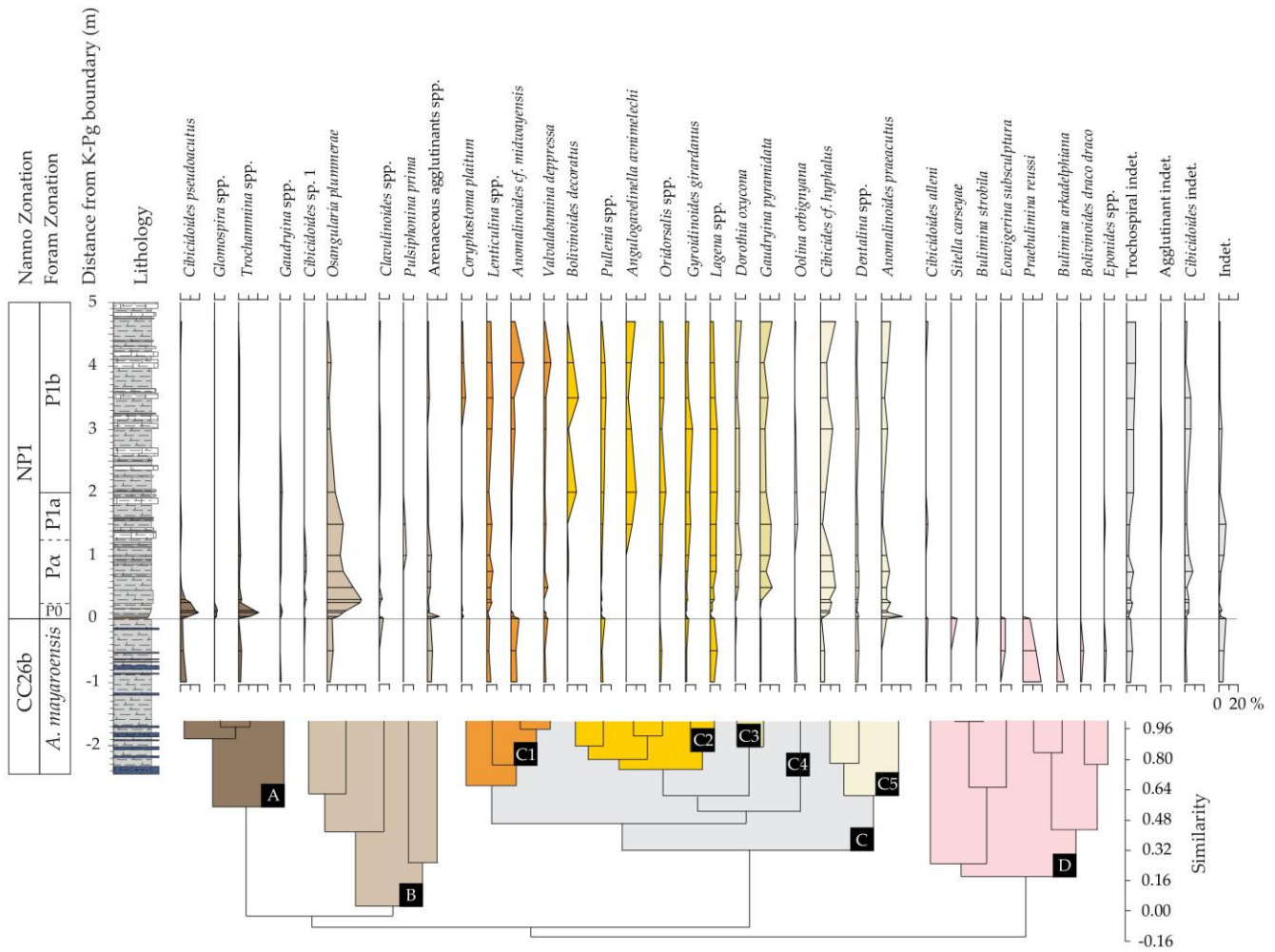


Figure 2: The benthic foraminiferal record of the Okçular section. The biostratigraphy is from Açıklın et al. (2015). A cluster analysis on the benthic foraminiferal data using paired group (UPGMA) correlation distance. This cluster analysis allows the identification of 4 main clusters of benthic foraminiferal taxa, clusters A to D.

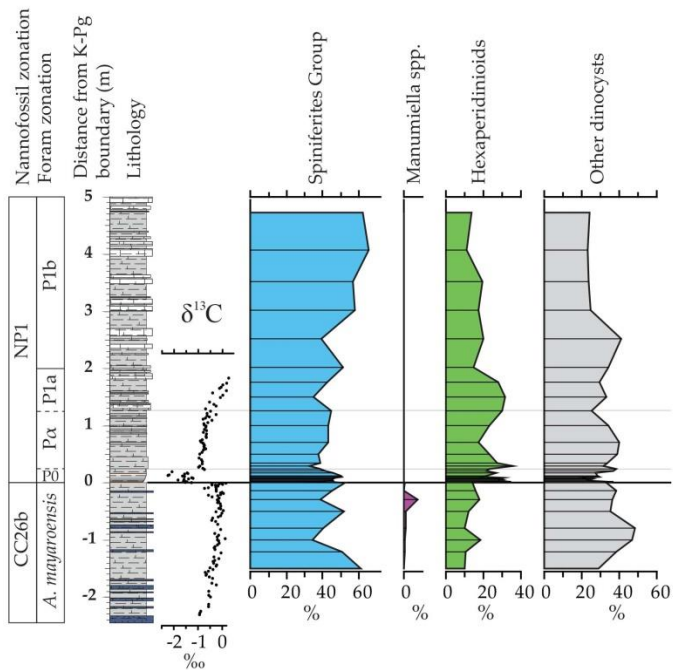


Figure 3: The organic-walled dinoflagellate cyst record of the Okçular section. The biostratigraphy and bulk carbonate stable carbon isotope record are from Açıkalın et al. (2015). The 4 main dinocyst complexes are indicated.

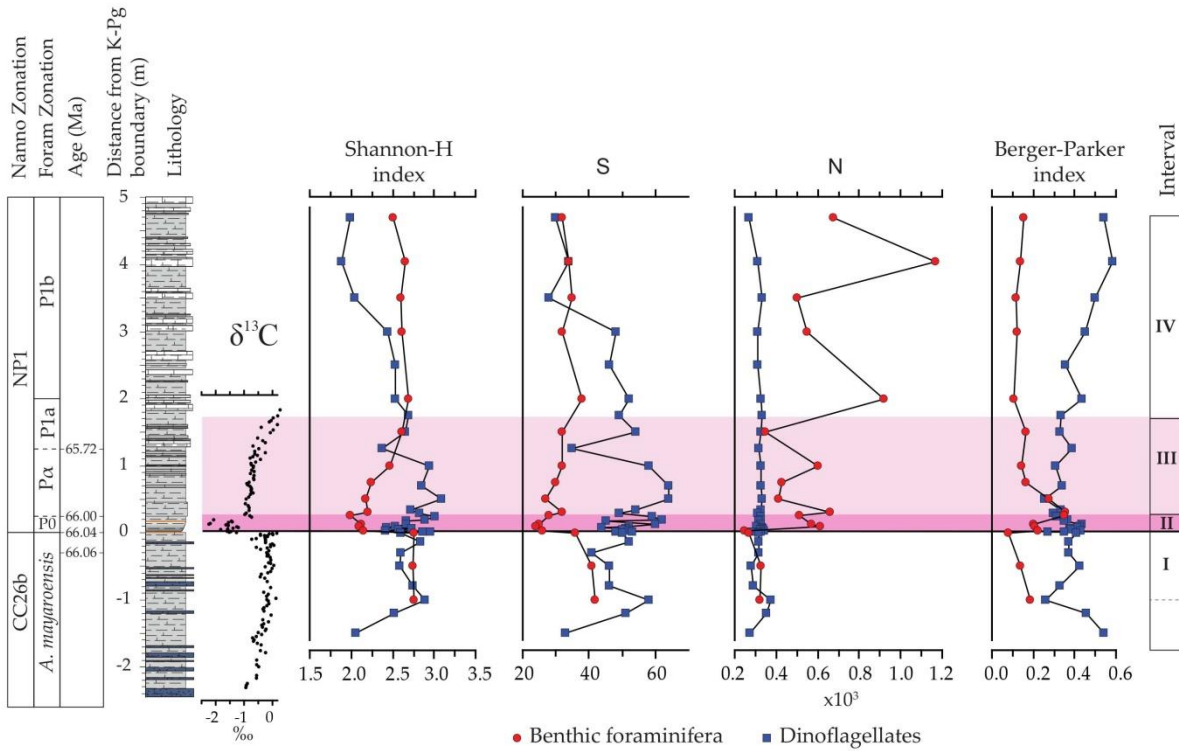
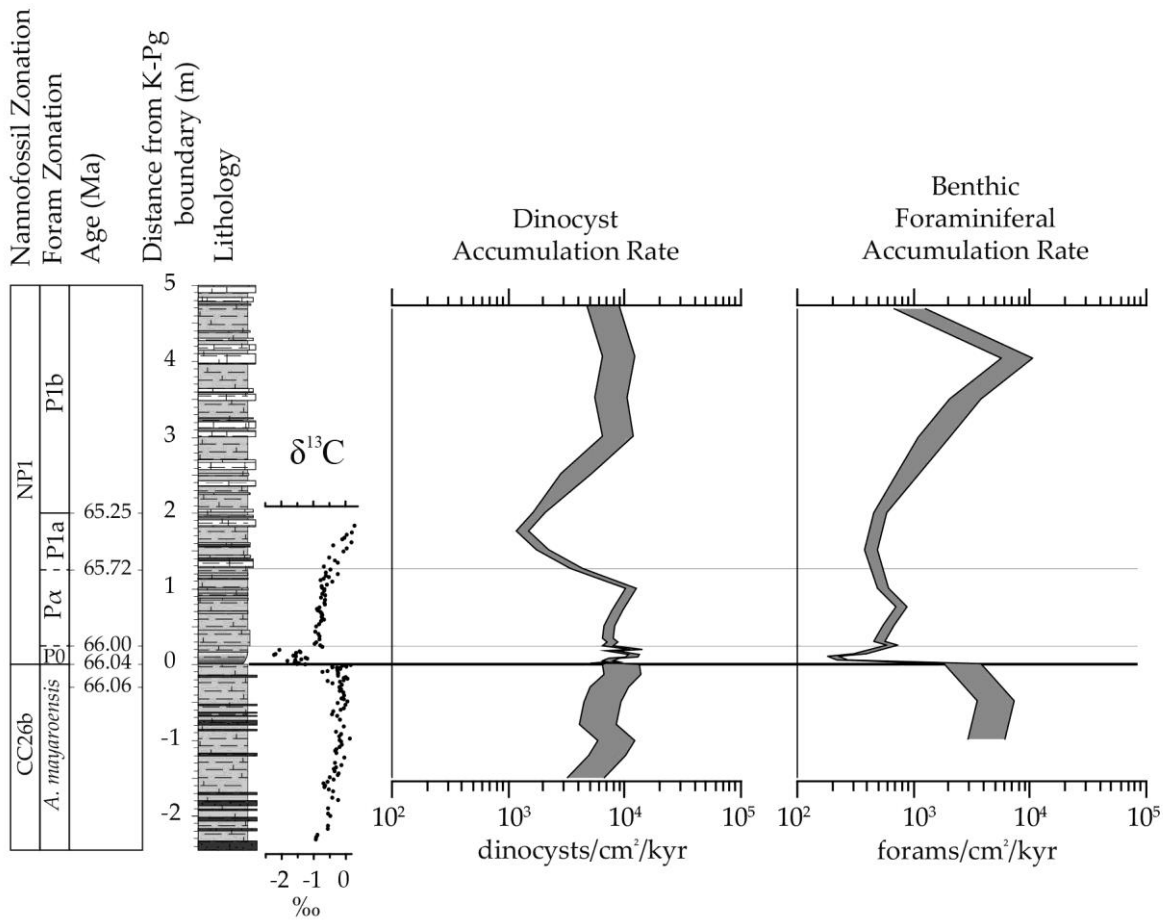


Figure 4: Diversity indices on the benthic foraminiferal and dinocyst records of the Okçular section, with the Shannon-H diversity index, the species richness per sample (S), number of specimen observed per sample (N) and the Berger-Parker Index. As the bulk stable carbon isotope record and the Shannon-H index of the benthic foraminiferal record show a similar trend, the combination of these records can be used to subdivide the K-Pg boundary transition into 4 intervals: I, the Maastrichtian, i.e. ‘pre-impact’ interval; II, the direct post-impact interval, representing the ‘disaster’ phase; III, a ‘recovery’ interval and IV, the Paleocene ‘post-recovery’ interval. The division criteria are explained in the text.



5 **Figure 5: Estimated Benthic Foraminiferal Accumulation Rate (BFAR; number of foraminifera of the >63 μ m size fraction per cm² sea floor per kyr) and estimated Dinocyst Accumulation Rate (DAR; number of preserved cysts per cm² sea floor per kyr) of the Okçular section. Uncertainty in estimated accumulation rates, resulting from uncertainties in sediment densities and sedimentation rates, is-are indicated in grey, providing a range of estimated accumulation rates. For more detailed info on the calculation of the BFAR and DAR, see Text S2 of the supplementary online material.**

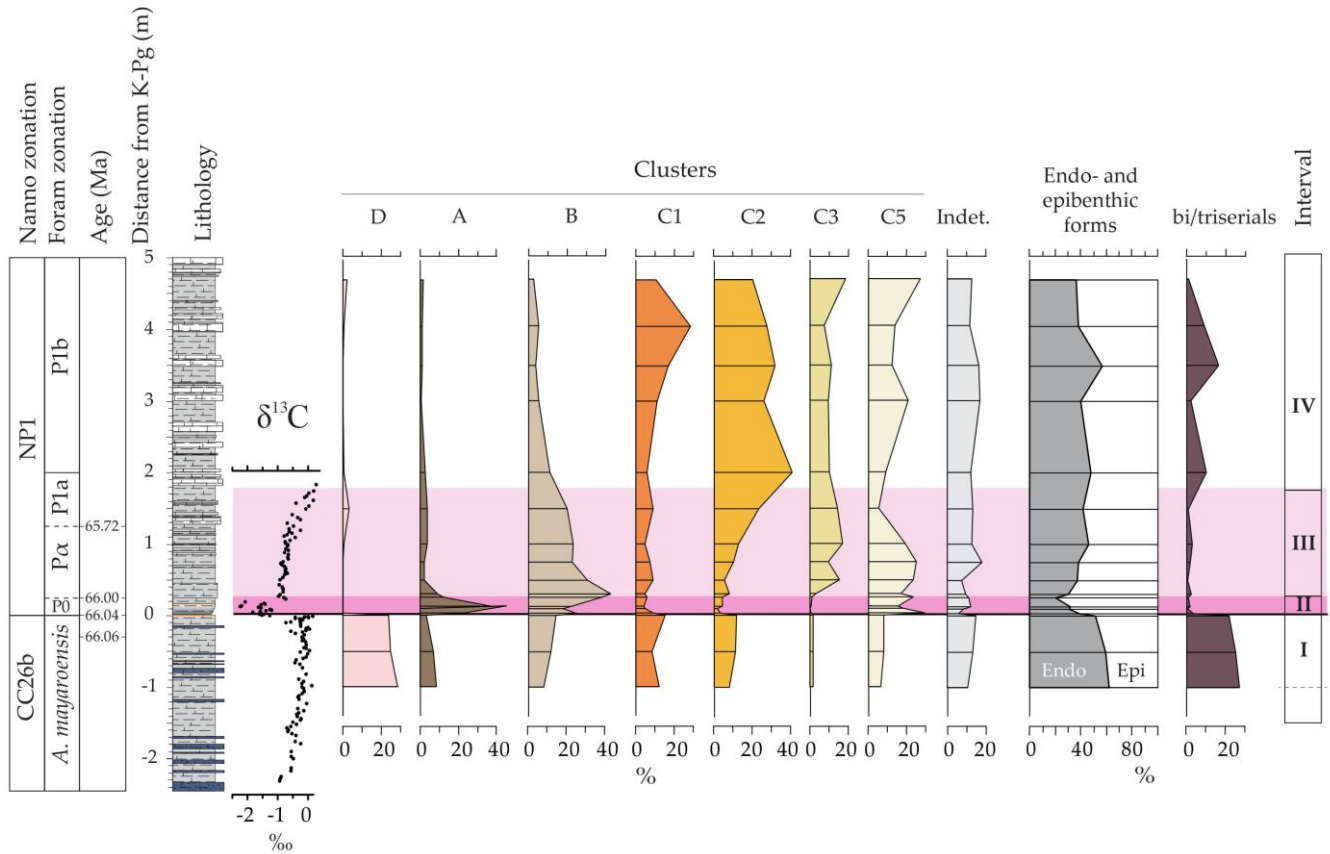


Figure 6: Relative abundances of the 4 main clusters of benthic foraminiferal taxa, relative abundances of epibenthic and endobenthic forms and relative abundance of bi-/triserial benthic taxa.

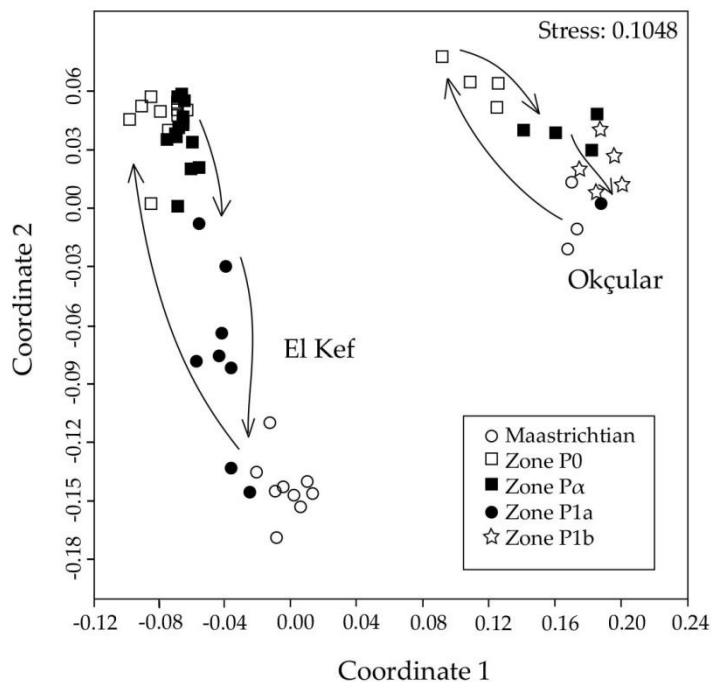


Figure 7: Q-mode Non-Metric Multi Dimensional Scaling (on all samples in the benthic foraminiferal dataset) of Okçular (this study) and El Kef (Speijer and van der Zwaan, 1996). After an abrupt transition from latest Maastrichtian pre-impact assemblage to disaster assemblage in the Zone P0 and recovery assemblage in Zone P α , a gradual transition towards a new equilibrium assemblage can be observed in Zones P1a and P1b.

5

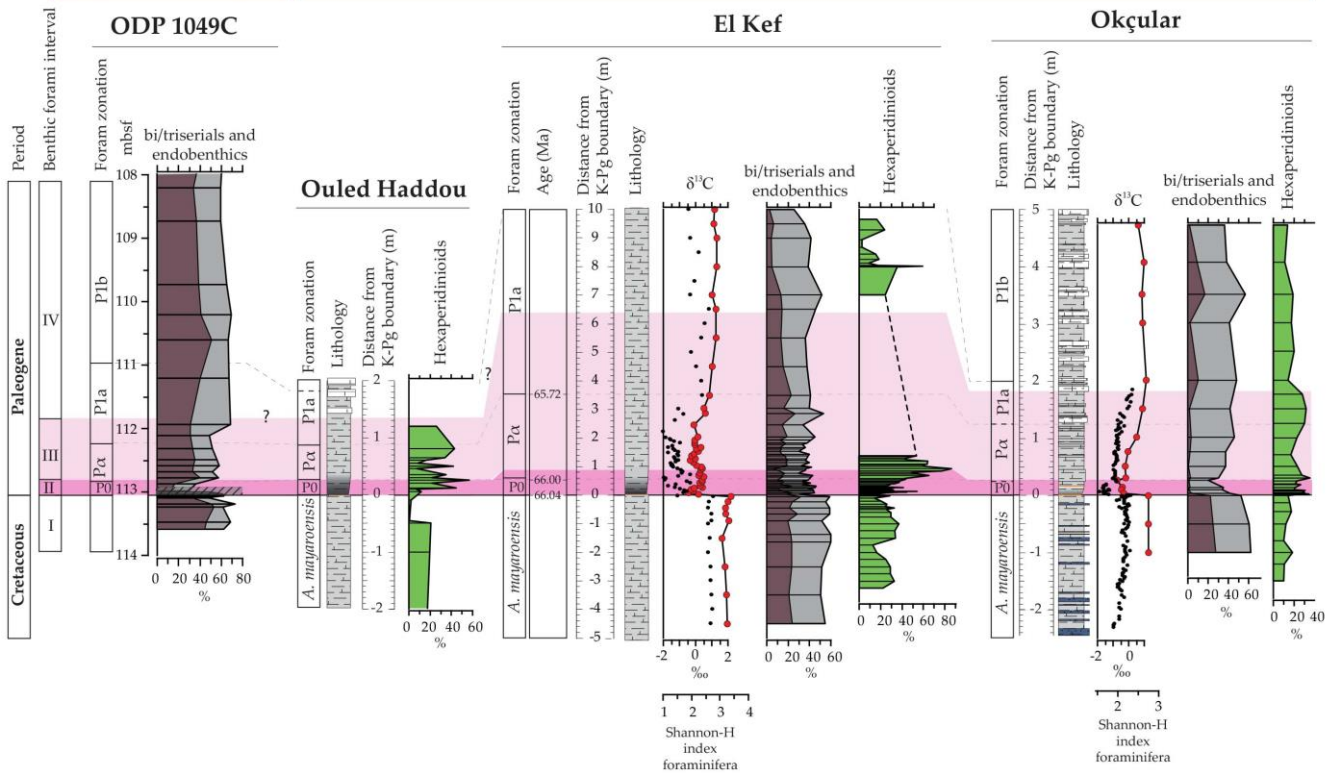


Figure 8: The benthic foraminiferal, dinocyst and bulk stable carbon isotope records of Okçular (Turkey) and El Kef (Tunisia), the dinocyst record of Ouled Haddou (Morocco) and the benthic foraminiferal record of ODP 1049C Blake Nose (North Atlantic). Note that the definition of ‘hexaperidinioids’ used is provided in the text. The 4 phases identified based on the bulk stable carbon isotopes and the Shannon-H index of the benthic foraminiferal records, are indicated (I-IV). The benthic foraminiferal record of ODP 1049C is from Alegret and Thomas (2004), who argued that the lowermost Paleocene of this site comprised reworked foraminifera. This interval is indicated by a dashed bar in the figure. The biostratigraphy of Ouled Haddou is from Slimani and Toufiq (2013), whereas the dinocyst record of this site is from Slimani et al. (2010). The biostratigraphy of El Kef is from Brinkhuis et al. (1998), Speijer and van der Zwaan (1996) and Molina et al. (2006). The fine fraction bulk stable carbon isotope record (black dots) of El Kef is from Keller and Lindinger (1989). The Shannon-H index (red dots) and relative abundances of bi-/triserial benthic taxa (dark purple) and all endobenthic foraminifera (light purple) are based on the foraminiferal data of Speijer and van der Zwaan (1996). The palynological data of El Kef is from Brinkhuis et al. (1998) (lower part) and Guasti et al. (2005) (upper part). The Shannon-H index of the benthic foraminiferal record (red dots), the relative contribution of bi-/triserial benthic taxa (dark purple), all endobenthic foraminifera (light purple) and hexaperidinioid dinocysts from Okçular are from this study. The bulk stable carbon isotope record of Okçular (black dots) is from Açikalin et al. (2015). Mbsf=meters below sea floor.

1
2 *Biogeosciences*

3 Supporting Information for

4 **Ecological response to collapse of the biological pump following the mass**
5 **extinction at the Cretaceous-Paleogene boundary**

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20
21 **Contents of this file**

22 Text S1

23 Text S2

24 [Text S3](#)

25 Figures S1 to ~~S4~~S3

26

27 **Additional Supporting Information (Files uploaded separately)**

28 Captions for Data Sets S1 and S2

29

30 **Introduction**

31 Supporting information includes additional information about the use of
32 hexaperidinioids as a qualitative proxy for nutrient availability (Text S1), ~~and~~ a
33 detailed description of the procedures followed to arrive at estimated benthic
34 foraminiferal accumulation rates and dinocyst accumulation rates for the
35 Cretaceous-Paleogene boundary interval of the Okçular section, Turkey (Text S2)
36 and a discussion on benthic foraminiferal diversity of the Okçular record (Text
37 S3). Supporting information also includes photo plates of the most common
38 benthic foraminiferal taxa (Figures S2-S3 and S34). Datasets provide benthic
39 foraminiferal and dinocyst counts (Data Sets S1 and S2). Details of the analyses
40 are explained in the Materials and Methods section in the main article.

41

42 **Text S1.**

43 Previous studies have shown that in the Tethys in particular the
44 hexaperidinioids show strong variations across the K-Pg boundary (Brinkhuis et
45 al., 1998; Vellekoop et al., 2015). Based on statistical correlations between
46 palynological records and other paleo-proxies, it has been suggested that this
47 inferred heterotrophic group is indicative of high nutrient availability and/or low
48 salinities. (Eshet et al., 1994; Brinkhuis et al., 1998; Sluijs and Brinkhuis, 2009).

49 Therefore, high abundances of this morphological group can be related to changes
50 in trophic condition as well as to changes in salinity. Since the Okçular section is
51 deposited at outer neritic to upper bathyal depths ([Açikalin et al., 2015](#)), this
52 locality probably represents a relatively distal setting, with little freshwater input.
53 Therefore, changes in relative abundances of hexaperidinioids are more likely to
54 reflect changes in nutrient availability rather than changes in salinity. To
55 nevertheless exclude the possibility that the signals in the palynological record can
56 be attributed to changes in freshwater input, we tested for a significant correlation
57 between relative abundances of hexaperidinioids and relative abundances of
58 terrestrial palynomorphs. Pollen and spores are land-derived and can therefore
59 be regarded as a proxy for the input of terrestrial-derived material. Since a
60 hypothetical decrease in salinity would most likely be associated with increased
61 riverine input, the input of terrestrial-derived material is expected to increase
62 with decreasing salinity.

63 Our correlation shows that there is no significant relationship between the
64 relative abundances of hexaperidinioids and the relative abundances of terrestrial
65 palynomorphs, $r(31) = 0.0089$, $p > 0.05$ (Figure S1). Therefore, in this study, high
66 abundances of hexaperidinioids are considered indicative of high nutrient
67 availability in the upper water column, instead increased freshwater input.

68

69 **Text S2.**

70 To estimate the Benthic Foraminiferal Accumulation Rate (BFAR, number of
71 [benthic](#) foraminifera per cm^2 per kyr), the number of benthic foraminifera
72 ($>63\mu\text{m}$) per gram [dry sediment](#) were calculated. In the foraminiferal records of
73 the Mudurnu-Göynük Basin there is a decrease in numbers of benthic foraminifera

74 across the K-Pg boundary, from 600-1200 foraminifera/gram in the Maastrichtian
75 to lowermost Danian values of 150-250 foraminifera/gram. Using the estimated
76 sedimentation rates for the studied interval based on the biostratigraphic age
77 model of Açikalin et al. (2015) and the estimated range of average densities for
78 the lithologies (mudstones, claystones and limestones) of the Tarakli Fm (2-2.5
79 g/cm³; Manger et al., 1963) the concentrations of foraminifera may be used to
80 estimate the BFAR. The resulting estimated BFAR record shows a drastic decrease
81 across the K-Pg boundary, from 1800-7200 foraminifera/cm²/kyr in the latest
82 Cretaceous to 175-400 foraminifera/cm²/kyr in the earliest Paleocene. The
83 benthic foraminiferal accumulation rate does not fully recover until Zone P1b.

84 To estimate the dinocyst accumulation rates, here defined as the preserved
85 cysts that accumulated per cm² sea floor per kyr, the dinocyst concentrations in
86 cysts per gram dry sediment were calculated. In the palynological records of the
87 Mudurnu-Göynük Basin there is a strong increase in concentrations of dinocysts
88 across the K-Pg boundary, from Maastrichtian abundances of ~1000-2000
89 cysts/gram at Okçular, to lowermost Danian values of up to ~14000 cysts/gram,
90 representing a 7 fold increase across the boundary. These high concentrations
91 occur in the interval correlative to planktic foraminiferal Zones P0 and P α , above
92 which concentrations decrease again to ~2500-6500 cysts/gram. Using the
93 estimated sedimentation rates for the studied interval based on the
94 biostratigraphic age model of Açikalin et al. (2015), the concentrations of
95 dinocysts (in cysts/cm²/gram) may be used to estimate the dinocyst
96 accumulation rates. The resulting records show that the estimated dinocyst
97 accumulation rate shows a general increasing trend across the boundary interval,
98 with no major changes at the boundary itself, implying that the change in absolute

99 concentrations of dinocysts at Okçular is mostly related to the decrease in
100 sedimentation rates across the K-Pg boundary (Açikalin et al., 2015).

101

102 **Text S3.**

103 Compared to the benthic foraminiferal records from the Bidart section (Alegret et
104 al., 2004), the Walvis Ridge section (Alegret and Thomas, 2007), the Agost section
105 (Alegret et al., 2003), and the El Kef section (Speijer and van der Zwaan, 1996), the
106 Fisher alpha and Shannon H diversity of the benthic foraminiferal assemblages are
107 lower in our study, also in the cases where the counted number of specimens is
108 higher than 600. It could be argued that the number of specimens in our study
109 (ranging from 245 to >500 specimens) may be too low to capture the full diversity
110 of our record. However, as Fisher-alpha should in theory not be sensitive to
111 number of specimens counted (Fisher et al., 1943), this is a strong indication that
112 diversity in our study is systematically lower than at these other sites.
113 Furthermore, when the number of species encountered in each sample is plotted
114 against the number of specimens counted per sample (SI, we see no trend towards
115 higher numbers of species with increasing sample size. We thus argue that we do
116 not have any indication that the number of specimens in our study may be too low
117 to capture the full diversity.

118

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157 continental shelf following the K-Pg boundary impact. *Palaeogeography, Palaeoclimatology,
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159

160

161 **Figure S1**

162 Relative abundances of hexaperidinioids of the Okçular section palynological samples

163 plotted against the relative abundances of sporomorphs within the same samples. This

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Met opmaak: Nederlands (standaard)

164 plot indicates that the variations of the relative abundances of hexaperidinioids are
165 likely not related to changes in freshwater input at this locality.

166
167 **Figure S2**

168 Number of specimens counted vs number of taxa encountered, for the 4 different
169 stratigraphic intervals. Both within each stratigraphic interval, as well as between the
170 different intervals, there is no clear relationship between number of specimens counted
171 and number of taxa encountered.

172
173 **Figure S3**

174 Plate 1. SEM images of most common benthic foraminifera found in this study.

- 175 1 a, b, c. *Angulogavelinella avnimelechi* (Reiss). Okçular, 150 cm.
176 2 a, b, c. *Anomalinoidea cf. midwayensis*. Okçular, -0.5 cm.
177 3 a, b, c. *Anomalinoidea praeacutus* (Vasilenko). Okçular, 8-9 cm.
178 4 a, b, c. *Cibicidoides cf. hyphalus*. Okçular, 49-50 cm.
179 5 a, b, c. *Cibicidoides pseudoacutus* (Nakkady). Okçular, 8-9 cm.
180 6 a, b, c. *Cibicidoides* sp. 1. Okçular, 74-75 cm.
181 7 a, b, c. *Valvulinerina depressa* (Alth). Okçular, 49-50 cm.
182 8 a, b, c. *Pulsiphonina prima* (Plummer). Okçular, 99-100 cm.
183 9 a, b, c. *Gyroidinoides girardanus* (Reuss). Okçular, 350 cm.
184 10 a, b, c. *Osangularia plummerae* (Brotzen). Okçular, 29-30 cm.

185
186 **Figure S4**

187 Plate 2. SEM images of most common benthic foraminifera found in this study.

- 188 11 a, b, c. *Cibicidoides alleni* (Plummer). Okçular, -0.5 cm.
189 12. *Bolivinoidea draco draco* (Marsson). Okçular, -50 cm.
190 13. *Bulimina arkadelphia* (Cushman and Parker). Okçular, -100 cm.

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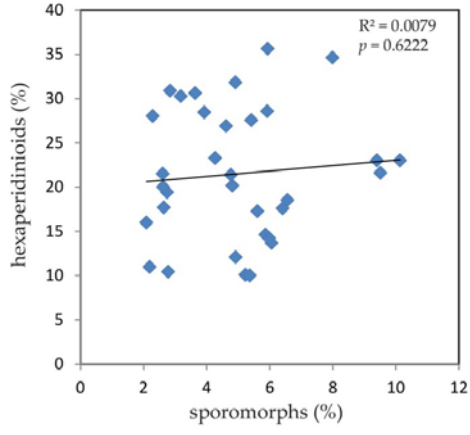
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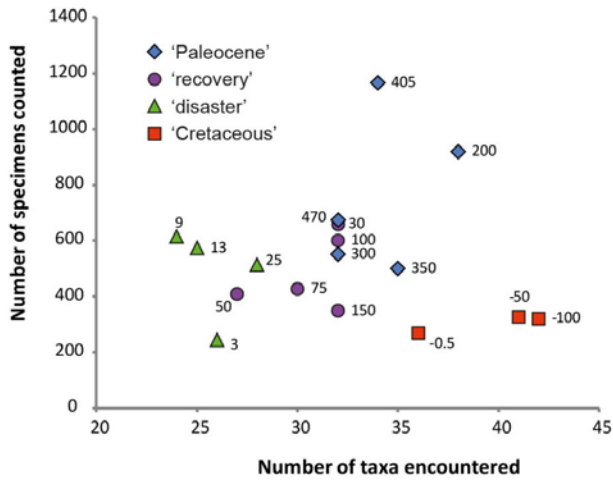
- 191 14. *Bulimina srobila* (Marie). Okçular, -0.5 cm.
192 15. *Sitella carseyae* (Plummer). Okçular, -0.5 cm.
193 16. *Eouvigerina subsculptura* (McNeil and Caldwell). Okçular, -50 cm.
194 17. *Coryphostoma midwayensis* (Cushman). Okçular, 350 cm.
195 18 a, b. *Dorothia oxycona* (Reuss). Okçular, 470 cm.
196 19. *Praebulimina reussi* (Morrow). Okçular, -100 cm.
197 20. *Gaudryina pyramidata* (Reuss). Okçular, 49-50 cm.
198 21. *Oolina orbignyana* (Kellough). Okçular, 150 cm.
199
200 .
201
202
203
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205 **Figure S1**



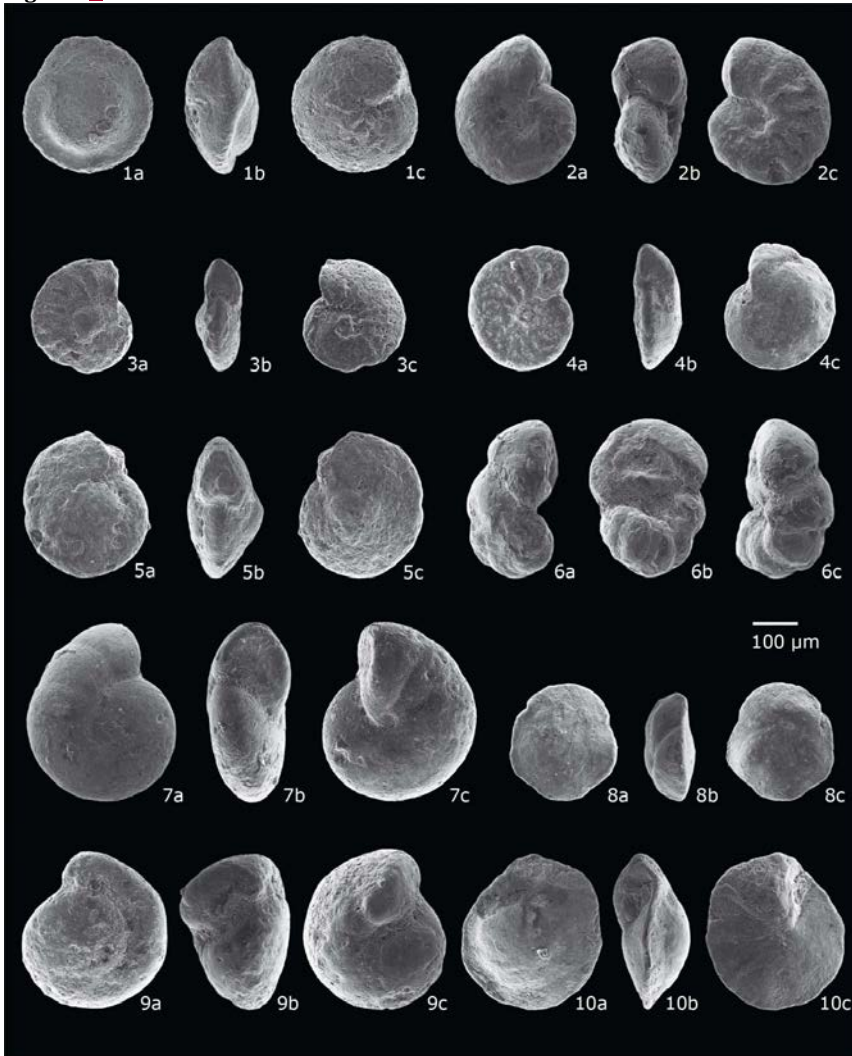
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Figure S2



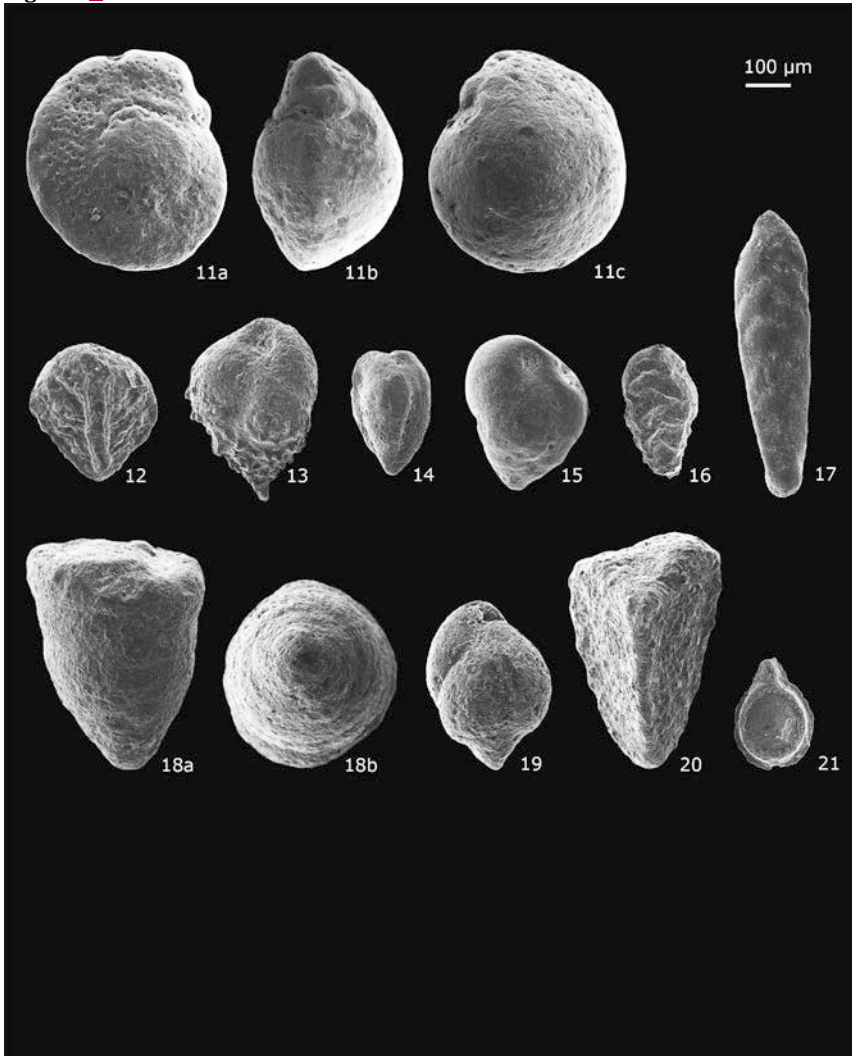
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216 **Figure S32**



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|221 **Figure S43**



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225 **Additional Supporting Information**

226 Captions for Data Sets S1 and S2
227

228 **Data Set S1**

229 Benthic foraminiferal counts of Okçular (Excell file)
230

231 **Data Set S2**

232 Palynological counts of Okçular (Excell file)
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