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Delayed calcareous nannoplankton boom-bust successions in the earliest Paleocene Chicxulub (Mexico) impact crater

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ABSTRACT

The Cretaceous-Paleogene (K-Pg; 66 Ma) mass extinction was caused by a bolide impact on the Yucatán platform near modern Chicxulub, Mexico. Calcareous nannoplankton, a dominant group of primary producers, were almost eradicated at this time. Post-impact nannoplankton assemblages from Northern Hemisphere sites were characterized by a short-lived series of high-dominance, low-diversity acmes (“boom-bust” successions), which likely represent an unstable post-impact environment. Although these boom-bust successions are a global signal, the mechanisms that controlled the taxonomic switchovers between acmes are currently unknown. Here, we present detailed analyses of calcareous nannoplankton and planktic foraminiferal assemblages in a new K-Pg section from the peak ring of the Chicxulub crater. We show that although nannoplankton assemblages resemble the typical series of acmes at Tethyan sites, the termination of the “disaster” acme in the crater is delayed by at least 500 k.y. The coincidence between shifts in the dominant planktic foraminiferal trophic group and switchovers in nannoplankton boom-bust taxa suggests that this series of acmes may represent a gradual trend toward oligotrophy driven by the global restoration of biological pump efficiency. Thus, the global diachroneity of boom-bust successions likely reflects the differential pacing of biological pump restoration between oceanic basins and settings.

INTRODUCTION

The bolide impact at the Cretaceous-Paleogene (K-Pg) boundary (ca. 66 Ma; e.g., Alvarez et al., 1980; Schulte et al., 2010) led to the extinction of ~75% of species on Earth (e.g., Jablonski, 1994), including 93% of calcareous nannoplankton (Bown, 2005). Due to their position at the base of the marine food web, the near-eradication of these dominant, unicellular primary producers likely led to large-scale shifts in trophic interactions and marine ecosystem dynamics (e.g., Solé et al., 2002; Hull et al., 2011).

The extinction of nannoplankton was selective, with most survivors adapted to high-nutrient (eutrophic) environments (Bown, 2005). In the Southern Hemisphere, extinction rates were lower, and early Danian assemblages were dominated by Cretaceous survivors (Schueth et al., 2015). In contrast, Northern Hemisphere nannoplankton communities experienced higher extinction rates, with post-extinction assemblages consisting of newly evolved species (Jiang et al., 2010). These taxa formed a series of short-lived (less than a few hundred thousand years), high-dominance, low-diversity acmes (Bown, 2005), which we term “boom-bust” successions after modern phytoplankton blooms (e.g., Winder and Cloern, 2010), although our geological examples have a far longer duration.

Boom-bust successions are interpreted as representing a series of adaptative radiations and migrations in an unstable post-impact environment (Hull et al., 2011). This instability may have included variable or extreme temperatures, pH, stratification, and/or nutrient concentrations, and their associated ecological interactions (e.g., competition and incumbency) (Bown, 2005; Schueth et al., 2015). Although it might be presumed that instability was prolonged and/or intensified at the site of the impact, the full diversity of planktic foraminifera appeared in the crater within years, while nannoplankton assemblages were of low abundance and diversity (Lowery et al., 2018). The rapid recovery of planktic foraminifera versus nannoplankton diversity suggests that it was ecological, not environmental, processes that drove recovery patterns.

Here we present the first detailed analyses of nannoplankton assemblages from the peak ring of the Chicxulub crater (International Ocean Discovery Program [IODP] Site M0077; Morgan et al., 2017). This site contains a stratigraphically continuous early Danian section (Lowery et al., 2018), which allows us to determine (1) whether the typical sequence of nannoplankton boom-bust acmes is observed at Chicxulub, (2) if the timing of acmes in the crater was substantially different from distal sites, and (3) which mechanisms drove the switchovers between acmes.

MATERIALS AND METHODS

Study Site

In 2016, the IODP and International Continental Drilling Program (ICDP) Expedition 364 recovered ~110 m of post-impact limestones from the peak ring of the Chicxulub impact crater (21.44993°N, 89.94947°W; Fig. 1). Here we present data from the base of these hemipelagic sediments (610.15–616.55 m below sea floor [mbsf]), but do not include the 76-cm-thick, higher-energy transitional unit that was the focus of Lowery et al. (2018). Nannoplankton smear slides and foraminifera samples were prepared using the methods outlined in Lowery et al. (2018). At least 200 nannoplankton specimens were identified to genus level and counted in each of the 84 samples, except where diversity and abundance were low. At least 300 individual planktic foraminifera were counted per sample.

Age Model

The age model used in this study is an updated version of that detailed by Morgan et al. (2017), which was constructed using planktic foraminifer biostratigraphy based on the “P” zones of Berggren and Pearson (2005) as updated by Wade et al. (2011). Calibrated ages were assigned to each datum using Gradstein et al. (2012), then estimated for each sample assuming constant sedimentation rates within each biozone (Tables DR1 and DR3 in the GSA Data

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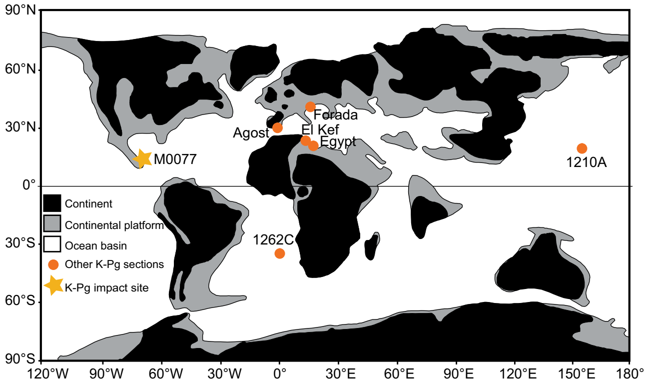

Figure 1. Paleogeographic map showing location of International Ocean Discovery Program (IODP) Site M0077 (Chicxulub impact crater, Mexico) relative to distal Cretaceous-Paleogene (K-Pg) sites used in this study (Agost, Spain [Pospichal, 1995]; Forada, Italy [Fornaciari et al., 2007]; El Kef, Tunisia [Pospichal, 1994]; Egypt [Tantawy, 2003]; Ocean Drilling Program (ODP) Site 1210A, Shatsky Rise, central Pacific Ocean [Bown, 2005]; and ODP Site 1262C, Walvis Ridge, southern Atlantic Ocean [Jiang et al., 2010]).

Repository[1]). The presence of all planktic foraminifer zonal markers and the lack of sedimentological evidence for hiatus indicate that the section is continuous (albeit condensed) for the first ~3 m.y. of the recovery. Nannoplankton assemblages in the crater were compared to those at Shatsky Rise (central Pacific Ocean; Bown, 2005) and Walvis Ridge (southern Atlantic Ocean; Jiang et al., 2010) using the cyclostratigraphic age models developed by Westerhold et al. (2008), and to those at Forada, Italy, by calibrating the "P" zones from Fornaciari et al. (2007) to age following Gradstein et al. (2012).

RESULTS

The earliest Danian nannoplankton assemblages at Site M0077 were dominated by calcareous dinoflagellate cysts (*Cervisiella* spp.; until recently called *Thoracosphaera* spp.) and *Braarudosphaera* spp. (Fig. 2). These low-diversity assemblages persisted for ~1 m.y. until the appearance of the *Futyania petalosa* acme, which lasted for ~500 k.y. From ~1.5 to 2.5 m.y. post-impact, nannoplankton assemblages were dominated by *Praeprinsius tenuiculus*. The termination of this acme marks the cessation of boom-bust successions, and the appearance of increased, relatively stable abundances of long-ranging Paleocene taxa including *Cruciplacolithus primus* and *Coccolithus pelagicus* (Fig. 2).

The relative dominance of planktic foraminiferal trophic groups also changed throughout the post-extinction interval (Fig. 2H). In the first 1 m.y. following the K-Pg boundary, assemblages were dominated by microperforates (e.g., *Guembelitria*, *Globoconusa*, *Parvularugoglobigerina*, *Woodringina*, and *Chiloguembelina*), with spinose forms (e.g., *Eoglobigerina* and the subbotinids) increasing in abundance from ~1 to 1.75 m.y. post-impact.

To compare nannoplankton recovery at Chicxulub to that of a group of published K-Pg boundary sections (Pospichal, 1994, 1995; Tantawy, 2003; Bown, 2005; Fornaciari et al., 2007; Jiang et al., 2010a) (Fig. 1), we used nonmetric multidimensional scaling (NMDS), an ordination technique that assesses dissimilarity between samples in large ecological data sets (Oksanen et al., 2018). Our results show that samples from different geographic regions occupy distinct areas of ordination space immediately after the impact (Fig. 3A), with earliest Danian assemblages at Chicxulub resembling those at most Tethyan sites (Agost, Spain [Pospichal, 1995]; Forada, Italy [Fornaciari et al., 2007]; and Wadi Hamama and Gebel Qreiya, Egypt [Tantawy, 2003]). These dissimilarities are largely driven by differences in the presence and dominance of specific opportunistic taxa such as *Cervisiella* spp., *Braarudosphaera* spp., and *Neobiscutum* spp. (Fig. 3B). Sample scores for all sites converge with time, showing that nannoplankton assemblages eventually became globally homogenous.

DISCUSSION

Calcareous Nannoplankton Assemblages in the Crater

For ~1 m.y. post-impact, assemblages in the crater were dominated by calcispheres (*Cervisiella* spp.), which proliferated globally as a response to harmful surface-water environments

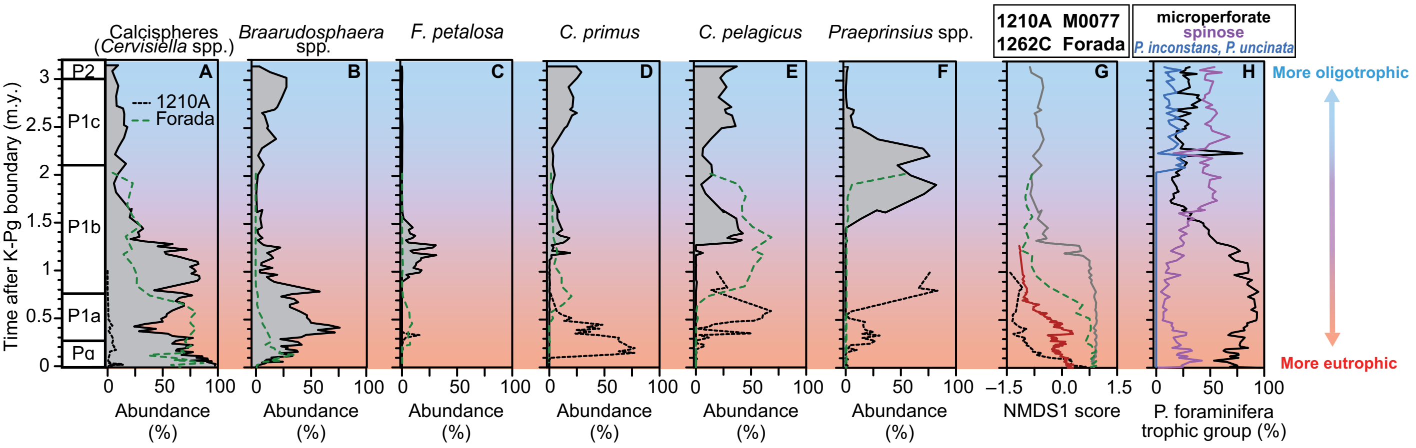

Figure 2. A–F: Relative abundance plots for nannoplankton taxa at International Ocean Discovery Program (IODP) Site M0077 (Chicxulub impact crater, Mexico) (this study; gray) compared to Forada, Italy (Fornaciari et al., 2007; dashed green line), and Ocean Drilling Program (ODP) Site 1210A, Shatsky Rise, central Pacific Ocean (Bown, 2005; dashed black line). Species abbreviations: *F. petalosa*—*Futyania petalosa*; *C. primus*—*Cruciplacolithus primus*; *C. pelagicus*—*Coccolithus pelagicus*. G: Nonmetric multidimensional scaling (NMDS) axis 1 sample scores (variability metric) for IODP Site M0077 (solid gray line); Forada (dashed green line); ODP Site 1210A, Shatsky Rise (dashed black line); and ODP Site 1262C, Walvis Ridge, southern Atlantic Ocean (solid red line). H: Relative abundance of planktic foraminiferal trophic groups at IODP Site M0077. *P.*—*Praemurica*; P. foraminifera—planktic foraminifera. Time after Cretaceous-Paleogene (K-Pg) boundary was estimated using cyclostratigraphy for Shatsky Rise and Walvis Ridge, and planktic foraminiferal biozones ("P" zones) of Berggren and Pearson (2005) as updated by Wade et al. (2011) for Chicxulub and Forada. Datums for base of "P" zones shown in figure are defined as follows: Pα—first occurrence (FO) of *Parvularugoglobigerina eugubina*; P1a—last occurrence (LO) of *Parvularugoglobigerina eugubina*; P1b—FO of *Subbotina triloculinoides*; P1c—FO of *Globanomalina compressa*; P2—FO of *Praemurica uncinata*.

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[1] GSA Data Repository item 2019271, Tables DR1–DR6 (data tables for Site M0077, and the age models used in this study (IODP Site M0077, Forada, and Shatsky Rise), and supplementary information discussing the possible effects of age model error, taxonomic issues, and preservation on our interpretations, is available online at http://www.geosociety.org/datarepository/2019/, or on request from editing@geosociety.org.

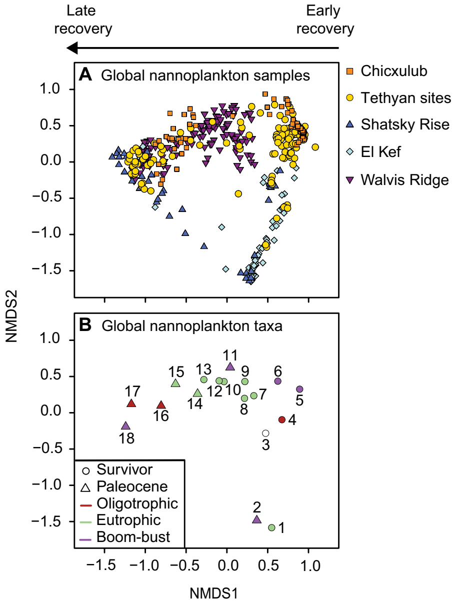

Figure 3. Nonmetric multidimensional scaling (NMDS) ordinations of global nannoplankton samples (A) and global nannoplankton taxa (B). The distance between scores along NMDS axes 1 and 2 are used as a measure of dissimilarity, with increasing distance between points representing greater dissimilarity. Data are from the Chicxulub impact crater, Mexico (this study); Agost, Spain (Pospichal, 1995); Wadi Hamama and Gebel Qreiya, Egypt (Tantawy, 2003); Forada, Italy (Fornaciari et al., 2007); El Kef, Tunisia (Pospichal, 1994); Ocean Drilling Program (ODP) Site 1210A, Shatsky Rise, central Pacific (Bown, 2005); and ODP Site 1262C, Walvis Ridge, southern Atlantic (Jiang et al., 2010). In B, species scores are for the following nannoplankton taxa: 1—*Lanternithus* spp.; 2—*Neobiscutum* spp.; 3—*Chiastozygus ultimus;* 4—*Watznaueria barnesiae*; 5—*Braarudosphaera* spp.; 6—*Cervisiella* spp. (calcispheres); 7—*Cyclagelosphaera reinhardtii*; 8—*Biscutum* spp.; 9—survivor holococcoliths; 10—*Markalius* spp.; 11—*Futyania petalosa*; 12—*Neocrepidolithus* spp.; 13—*Zeugrhabdotus sigmoides*; 14—*Hornibrookina* spp.; 15—*Neochiastozygus* spp.; 16—*Cruciplacolithus* spp.; 17—*Coccolithus* and *Ericsonia* spp.; 18—*Praeprinsius* and *Prinsius* spp. Survivor refers to the nannoplankton taxa that survived the Cretaceous-Paleogene mass extinction event, and Paleogene refers to the nannoplankton taxa that originated in the earliest Danian. Ecological preferences for each taxon follow those listed in Jiang et al. (2010). Please note that we also consider earlier short-lived acmes of *Cruciplacolithus primus* and *Coccolithus pelagicus* to be part of boom-bust successions. Unfilled symbols indicate nannoplankton taxa with uncertain ecology.

(e.g., Brinkhuis et al., 1998; Vellekoop et al., 2015). *Braarudosphaera* spp. were also a major component of nannoplankton assemblages throughout the post-extinction interval (Fig. 2B). This Cretaceous survivor is adapted to unstable, eutrophic environments, and formed geographically restricted acmes after the K-Pg boundary (e.g., Fornaciari et al., 2007; Lamolda et al., 2016). Due to the abundance of these opportunistic taxa, the composition of assemblages at Chicxulub resembles that at most Tethyan sites (Figs. 2A–2B and 3A). However, *Braarudosphaera* spp. were more dominant in the crater and persisted for longer (Fig. 2B), suggesting that eco-physiological conditions were optimal for this taxon at Chicxulub. In contrast, assemblages at El Kef (Tunisia) and Shatsky Rise contained few *Braarudosphaera* spp., with abundant calcispheres only immediately above the boundary (Figs. 2B and 3A). Instead, assemblages at these sites were dominated by *Neobiscutum parvulum* (Bown 2005; Fig. 3), which also occurred immediately after the "disaster" acme at many Tethyan sites (e.g., Lamolda et al., 2016).

By 1 m.y. post-impact, nannoplankton assemblages in the crater were characterized by successive acmes of the newly evolved taxa *F. petalosa* and *P. tenuiculus* (Fig. 2). Although these resemble the boom-bust successions at other Northern Hemisphere sites, the dominance, timing, and nature of each acme varied. For example, the dominant *C. pelagicus* and *C. primus* acmes observed at Shatsky Rise and Forada were poorly defined at Chicxulub. Furthermore, these acmes occurred at least 250 k.y. earlier at Shatsky Rise than at Forada. In contrast, the *F. petalosa* acme was much more dominant in the crater but occurred ~500 k.y. after it did at the other two sites. Surprisingly, the initiation of the *P. tenuiculus* acme was almost coincident at Chicxulub and Forada, but occurred ~1 m.y. earlier at Shatsky Rise, suggesting a more rapid biotic recovery in this open-marine ocean basin. By ~3 m.y. post-impact, stable populations of long-ranging Paleocene taxa were present at most sites (Fig. 3A), signaling the end of post-extinction ecosystem instability and heterogeneity.

Diachronous nannoplankton acmes are also observed in the NMDS axis 1 sample scores (Fig. 2G), which reveal a geographically asynchronous transition from assemblages dominated by opportunistic taxa (high NMDS1 sample scores) to those with abundant, long-ranging Paleocene species (low NMDS1 sample scores). This transition occurs first at Shatsky Rise (~100 k.y. post-impact), followed by Walvis Ridge (~400 k.y. post-impact), Forada (~700 k.y. post-impact), and Chicxulub (~1 m.y. post-impact). Thus, these results support the hypothesis that newly evolved Paleocene taxa originated in the Pacific Ocean before migrating to other ocean basins (Schueth et al., 2015).

The observed diachroneity is unlikely to be an artifact of differences in nannoplankton preservation and taxonomy because boom-bust taxa were mostly compared at the genus level. The scale of the diachroneity can also not be completely explained by asynchronous planktic foraminiferal biozone markers. Comparison of the timing of nannoplankton acmes at Shatsky Rise and Walvis Ridge using orbital chronology (Westerhold et al., 2008) and poorly constrained biostratigraphic datums suggests a maximum age model–derived error of 100 k.y. (see full discussion in the Data Repository). Therefore, we are confident that the broad, global, asynchronous evolution of post-extinction nannoplankton assemblages is a real signal that represents environmental and ecological differences between oceanic basins and settings.

What Drove Nannoplankton Boom-Bust Successions?

Although nannoplankton boom-bust successions are global, their significance is poorly understood. Remarkably, our data demonstrate that the switchovers between nannoplankton acmes closely track shifts in planktic foraminiferal trophic groups at Chicxulub (Fig. 2). The dominance of eutrophic microperforate foraminifera in the crater coincides with acmes of the opportunistic nannoplankton taxa *Cervisiella* spp. and *Braarudosphaera* spp. (Figs. 2A, 2B, and 2H), both of which are adapted to eutrophic conditions. The existence of high-nutrient surface waters is supported by Ba/Ti values in the crater, which indicate enhanced export productivity in the earliest Paleocene (Lowery et al., 2018). From ~1 to 1.5 m.y. post-impact, there is a switchover in dominance between microperforate and spinose foraminifera, which were able to catch motile prey (Olsson et al., 1992) and likely thrived in more oligotrophic environments. This interval encompasses the range of *F. petalosa*, a nannoplankton species with a previously unknown paleoecology. Although the diversification of symbiont-bearing foraminifera occurred just above our study interval, we interpret higher abundances of *Praemurica inconstans* and *P. uncinata* (the first species to acquire photosymbionts; Norris, 1996) at ~2 m.y. as evidence for a further increase in oligotrophy. This corresponds to increased abundances of *P. tenuiculus* and long-ranging Paleocene species such as *C. pelagicus* and *C. primus* which are generally considered oligotrophic (e.g., Jiang et al., 2010). Therefore, we suggest that a gradual transition to more oligotrophic conditions led to a series of adaptations which caused one taxon to become dominant for hundreds of thousands of years, until another, rarer taxon became better adapted and increased rapidly in abundance (i.e., boom-bust successions).

Previous work has shown that the evolution and dominance of planktic foraminiferal trophic strategies track stages in the global collapse and subsequent restoration of the marine biological pump (the export productivity of carbon from the surface to the deep ocean [Kump, 1991]) (Coxall et al., 2006; Hull et al., 2011; Birch et al., 2016). Because the taxonomic switchovers between nannoplankton acmes coincide with changes in the dominant planktic foraminiferal trophic group, we postulate that nannoplankton boom-bust successions are also a response to biological pump recovery. Immediately after the mass extinction event, less efficient export productivity and thus enhanced remineralization of organic matter in the surface ocean would have favored the survival and proliferation of eutrophic taxa. New Paleocene taxa likely migrated into the crater geologically rapidly due to the crater's open connection with the Gulf of Mexico (Gulick et al., 2008). However, their abundances would have remained low until biological pump efficiency increased, surface-water nutrient concentrations decreased, and eutrophic, opportunistic survivors were displaced. The subsequent boom-bust taxa may each have had slightly different ecological preferences, allowing specific taxa to be more competitive at various stages in the recovery of biological pump efficiency.

Long-term geographic variability in export productivity has been well documented following the K-Pg boundary (Hull and Norris, 2011), and likely reflects differential rates in the recovery of biological pump efficiency. Therefore, we suggest that the diachronous timing of nannoplankton boom-bust successions was similarly related to asynchronous biological pump recovery. Collapse of the biological pump would have particularly enhanced eutrophication at shallower, high-productivity sites influenced by nutrient input from land, favoring the dominance and persistence (i.e., incumbency) of opportunistic eutrophic taxa. This may have restricted the proliferation of newly evolved taxa at Chicxulub and the Tethyan sites, thus leading to the delay in boom-bust successions. In contrast, contemporaneous assemblages in lower-nutrient, open-ocean settings were characterized by well-defined acmes of the oligotrophic species *C. primus* and *C. pelagicus*. This indicates that ecosystem instability was shorter lived in the open ocean, perhaps due to the more rapid restoration of biological pump efficiency.

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REFERENCES CITED

Alvarez, L.W., Alvarez, W., Asaro, F., and Michel, H.V., 1980, Extraterrestrial cause for the Cretaceous-Tertiary extinction: Science, v. 208, p. 1095–1108, https://doi.org/10.1126/science.208.4448.1095.

Berggren, W.A., and Pearson, P.N., 2005, A revised tropical to subtropical Paleogene planktonic foraminiferal zonation: Journal of Foraminiferal Research, v. 35, p. 279–298, https://doi.org/10.2113/35.4.279.

Birch, H.S., Coxall, H.K., Pearson, P.N., Kroon, D., and Schmidt, D.N., 2016, Partial collapse of the marine carbon pump after the Cretaceous-Paleogene boundary: Geology, v. 44, p. 287–290, https://doi.org/10.1130/G37581.1.

Bown, P., 2005, Selective calcareous nannoplankton survivorship at the Cretaceous-Tertiary boundary: Geology, v. 33, p. 653–656, https://doi.org/10.1130/G21566.1.

Brinkhuis, H., Bujak, J.P., Smit, J., Versteegh, G.J.M., and Visscher, H., 1998, Dinoflagellate-based sea surface temperature reconstructions across the Cretaceous-Tertiary boundary: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 141, p. 67–83, https://doi.org/10.1016/S0031-0182(98)00004-2.

Coxall, H.K., D'Hondt, S., and Zachos, J.C., 2006, Pelagic evolution and environmental recovery after the Cretaceous-Paleogene mass extinction: Geology, v. 34, p. 297–300, https://doi.org/10.1130/G21702.1.

Fornaciari, E., Giusberti, L., Luciani, V., Tateo, F., Agnini, C., Backman, J., Oddone, M., and Rio, D., 2007, An expanded Cretaceous–Tertiary transition in a pelagic setting of the Southern Alps (central-western Tethys): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 255, p. 98–131, https://doi.org/10.1016/j.palaeo.2007.02.044.

Gradstein, F.M., Ogg, J.G., Schmitz, M.D., and Ogg, G.M., eds., 2012, The Geological Time Scale 2012: Amsterdam, Elsevier, 1176 p.

Gulick, S.P., et al., 2008, Importance of pre-impact crustal structure for the asymmetry of the Chicxulub impact crater: Nature Geoscience, v. 1, p. 131–135, https://doi.org/10.1038/ngeo103.

Hull, P.M., and Norris, R.D., 2011, Diverse patterns of ocean export productivity change across the Cretaceous-Paleogene boundary: New insights from biogenic barium: Paleoceanography and Paleoclimatology, v. 26, PA3205, https://doi.org/10.1029/2010PA002082.

Hull, P.M., Norris, R.D., Bralower, T.J., and Schueth, J.D., 2011, A role for chance in marine recovery from the end-Cretaceous extinction: Nature Geoscience, v. 4, p. 856–860, https://doi.org/10.1038/ngeo1302.

Jablonski, D., 1994, Extinctions in the fossil record: Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, v. 344, p. 11–17, https://doi.org/10.1098/rstb.1994.0045.

Jiang, S., Bralower, T.J., Patzkowsky, M.E., Kump, L.R., and Schueth, J.D., 2010, Geographic controls on nannoplankton extinction across the Cretaceous/Palaeogene boundary: Nature Geoscience, v. 3, p. 280–285, https://doi.org/10.1038/ngeo775.

Kump, L.R., 1991, Interpreting carbon-isotope excursions: Strangelove oceans: Geology, v. 19, p. 299–302, https://doi.org/10.1130/0091-7613(1991)019<0299:ICIESO>2.3.CO;2.

Lamolda, M.A., Melinte-Dobrinescu, M.C., and Kaiho, K., 2016, Calcareous nannoplankton assemblage changes linked to paleoenvironmental deterioration and recovery across the Cretaceous–Paleogene boundary in the Betic Cordillera (Agost, Spain): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 441, p. 438–452, https://doi.org/10.1016/j.palaeo.2015.10.003.

Lowery, C.M., et al., 2018, Rapid recovery of life at ground zero of the end-Cretaceous mass extinction: Nature, v. 558, p. 288–291, https://doi.org/10.1038/s41586-018-0163-6.

Morgan, J., Gulick, S., Mellett, C.L., Green, S.L., and the Expedition 364 Scientists, 2017, Proceedings of the International Ocean Discovery Program, Volume 364: Chicxulub: Drilling the K-Pg Impact Crater: College Station, Texas, International Ocean Discovery Program, https://doi.org/10.14379/iodp.proc.364.2017.

Norris, R.D., 1996, Symbiosis as an evolutionary innovation in the radiation of Paleocene planktic foraminifera: Paleobiology, v. 22, p. 461–480, https://doi.org/10.1017/S0094837300016468.

Oksanen, J., et al., 2018, vegan: Community Ecology Package, version 2.4-2, *in* R: A Language and Environment for Statistical Computing: R Core Team, https://cran.r-project.org/package=vegan.

Olsson, R.K., Hemleben, C., Berggren, W.A., and Liu, C., 1992, Wall texture classification of planktonic foraminifera genera in the lower Danian: Journal of Foraminiferal Research, v. 22, p. 195–213, https://doi.org/10.2113/gsjfr.22.3.195.

Pospichal, J.J., 1994, Calcareous nannofossils at the K-T boundary, El Kef: No evidence for stepwise, gradual, or sequential extinctions: Geology, v. 22, p. 99–102, https://doi.org/10.1130/0091-7613(1994)022<0099:CNATKT>2.3.CO;2.

Pospichal, J.J., 1995, Cretaceous/Tertiary boundary calcareous nannofossils from Agost, Spain, *in* Flores, J.A., and Sierro, F.J., eds., Proceedings of the 5th International Nannoplankton Association Conference in Salamanca: Salamanca, Universidad de Salamanca Press, p. 185–217.

Schueth, J.D., Bralower, T.J., Jiang, S., and Patzkowsky, M.E., 2015, The role of regional survivor incumbency in the evolutionary recovery of calcareous nannoplankton from the Cretaceous/Paleogene (K/Pg) mass extinction: Paleobiology, v. 41, p. 661–679, https://doi.org/10.1017/pab.2015.28.

Schulte, P., et al., 2010, The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary: Science, v. 327, p. 1214–1218, https://doi.org/10.1126/science.1177265.

Solé, R.V., Montoya, J.M., and Erwin, D.H., 2002, Recovery after mass extinction: Evolutionary assembly in large-scale biosphere dynamics: Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, v. 357, p. 697–707, https://doi.org/10.1098/rstb.2001.0987.

Tantawy, A.A.A.M., 2003, Calcareous nannofossil biostratigraphy and paleoecology of the Cretaceous–Tertiary transition in the central eastern desert of Egypt: Marine Micropaleontology, v. 47, p. 323–356, https://doi.org/10.1016/S0377-8398(02)00135-4.

Vellekoop, J., Smit, J., van de Schootbrugge, B., Weijers, J.W.H., Galeotti, S., Sinninghe Damsté, J.S., and Brinkhuis, H., 2015, Palynological evidence for prolonged cooling along the Tunisian continental shelf following the K-Pg boundary impact: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 426, p. 216–228, https://doi.org/10.1016/j.palaeo.2015.03.021.

Wade, B.S., Pearson, P.N., Berggren, W.A., and Pälike, H., 2011, Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale: Earth-Science Reviews, v. 104, p. 111–142, https://doi.org/10.1016/j.earscirev.2010.09.003.

Westerhold, T., Röhl, U., Raffi, I., Fornaciari, E., Monechi, S., Reale, V., Bowles, J., and Evans, H.F., 2008, Astronomical calibration of the Paleocene time: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 257, p. 377–403, https://doi.org/10.1016/j.palaeo.2007.09.016.

Winder, M., and Cloern, J.E., 2010, The annual cycles of phytoplankton biomass: Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, v. 365, p. 3215–3226, https://doi.org/10.1098/rstb.2010.0125.

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