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Rapid macrobenthic diversification and stabilization after the end-Cretaceous mass extinction event

Francisco J. Rodríguez-Tovar[1]*, Christopher M. Lowery[2], Timothy J. Bralower[3], Sean P.S. Gulick[2,4,5] and Heather L. Jones[3]
[1]Departamento de Estratigrafía y Paleontología, Universidad de Granada, 18002 Granada, Spain
[2]Institute for Geophysics, Jackson School of Geosciences, University of Texas at Austin, Austin, Texas 78758, USA
[3]Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802, USA
[4]Center for Planetary Systems Habitability, University of Texas at Austin, Austin, Texas 78712, USA
[5]Department of Geological Sciences, Jackson School of Geosciences, University of Texas at Austin, Austin, Texas 78712, USA

ABSTRACT

Previous ichnological analysis at the Chicxulub impact crater, Yucatán Peninsula, México (International Ocean Discovery Program [IODP]/International Continental Scientific Drilling Program [ICDP] Site M0077), showed a surprisingly rapid initial tracemaker community recovery after the end-Cretaceous (Cretaceous-Paleogene [K-Pg]) mass extinction event. Here, we found that full recovery was also rapid, with the establishment of a well-developed tiered community within ~700 k.y. Several stages of recovery were observed, with distinct phases of stabilization and diversification, ending in the development of a trace fossil assemblage mainly consisting of abundant *Zoophycos*, *Chondrites*, and *Planolites*, assigned to the *Zoophycos* ichnofacies. The increase in diversity is associated with higher abundance, larger forms, and a deeper and more complex tiering structure. Such rapid recovery suggests that favorable paleoenvironmental conditions were quickly reestablished within the impact basin, enabling colonization of the substrate. Comparison with the end-Permian extinction reveals similarities during recovery, yet postextinction recovery was significantly faster after the K-Pg event. The rapid recovery has significant implications for the evolution of macrobenthic biota after the K-Pg event. Our results have relevance in understanding how communities recovered after the K-Pg impact and how this event differed from other mass extinction events.

INTRODUCTION

Mass extinction events punctuated the Phanerozoic and dramatically affected evolution on Earth. The aftermath of a mass extinction event is an extraordinary phase in evolutionary history, and understanding the nature and timing of biotic recovery is a fundamental challenge. The end-Cretaceous (Cretaceous-Paleogene [K-Pg]) mass extinction, 66.0 m.y. ago (Renne et al., 2013), was one of the most important events in the Phanerozoic, severely altering the evolutionary and ecological history of biotas (Schulte et al., 2010). This extinction was caused by paleoenvironmental changes associated with the impact of an asteroid (Alvarez et al., 1980) on the Yucatán carbonate-evaporite platform in the southern Gulf of Mexico, which formed the Chicxulub impact crater (Hildebrand et al., 1991). In the aftermath of the K-Pg mass extinction, the biological pump that facilitates the downward flux of organic matter was weakened (Birch et al., 2016), and global export production declined in many places (Hull et al., 2011). The final global recovery of the biological pump occurred ~2–3 m.y. after the transition (Birch et al., 2016). The effect of these changes on the macrobenthic community is poorly known. Ichnological analyses conducted on distal marine K-Pg boundary sections worldwide revealed a relatively diverse ichnoassemblage just above the ejecta layer, and a minor effect on the tracemaker community (Labandeira et al., 2016). This assemblage mainly consists of *Chondrites*, *Zoophycos*, *Planolites*, and *Thalassinoides*, characterizing a multitiered ichnofauna from the *Zoophycos* ichnofacies (e.g., Rodríguez-Tovar and Uchman, 2004, 2006; Rodríguez-Tovar, 2005; Monaco et al., 2015).

We studied a continuous, extended record of postimpact sedimentary rocks from the peak ring of the Chicxulub impact crater, Yucatán Peninsula, México (International Ocean Discovery Program [IODP]/International Continental Scientific Drilling Program [ICDP] Site M0077), recovered during the ICDP Expedition 364 (Morgan et al., 2016). The location of the impact was a carbonate ramp with an average water depth of 600 m (Gulick et al., 2008). The depositional environment during the early Paleocene at Site M0077 corresponded to the upper and/or middle bathyal zone at ~600–700 m depth (Lowery et al., 2018).

Export production in the newly formed Chicxulub crater was high until ~300 k.y. after the impact, and then it slowly declined through 1 m.y. postimpact, initiating a turnover in calcareous nannoplankton assemblages (Jones et al., 2019). The initial biologic recovery at the Chicxulub impact crater revealed that the reappearance of life occurred within years of the impact (Lowery et al., 2018); at the base of the postimpact section, *Planolites*, *Chondrites*, and *Palaeophycus* are observed. However, the absence of *Zoophycos* is evidence that the community had not yet been fully established. Here, we describe the results of a detailed ichnological analysis of postimpact Paleocene sediments (the overlying 2.6 m; Fig. S1 in the Supplemental Material[1]) to interpret the variation in the macrobenthic tracemaker community and then determine how long it took for assemblages typical of the *Zoophycos* ichnofacies to be completely established postimpact. This interval corresponds to the early Paleocene (planktic

*E-mail: fjrtovar@ugr.es

[1]Supplemental Material. Method details for ichnological analysis and age calibration, Figures S1 and S2, and Table S1. Please visit https://doi.org/10.1130/GEOL.S.12501839 to access the supplemental material, and contact editing@geosociety.org with any questions.

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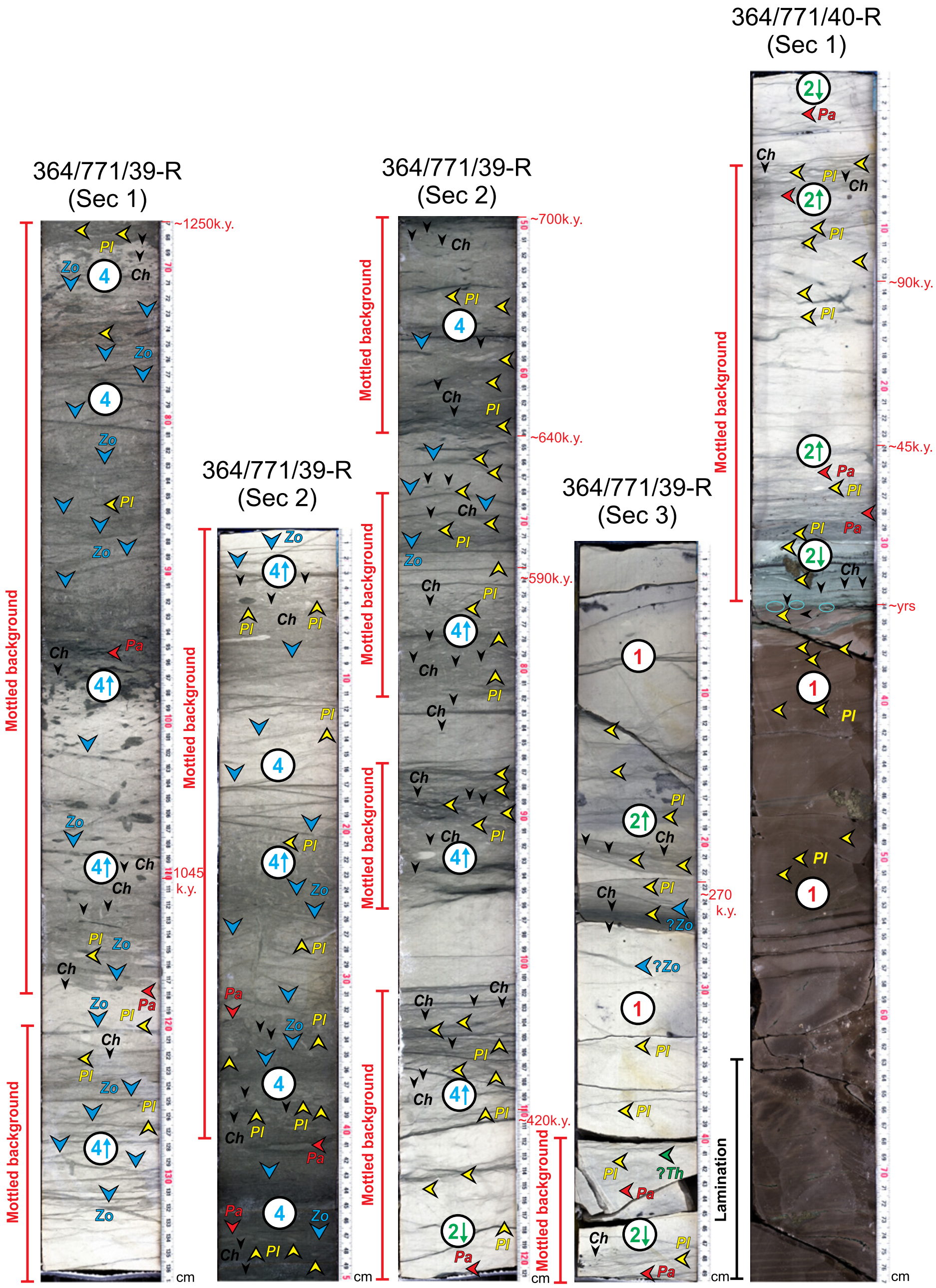

Figure 1. Sedimentological and ichnological features through the studied cores, from the Chicxulub impact crater, Yucatán Peninsula, México (International Ocean Discovery Program [IODP]/International Continental Scientific Drilling Program [ICDP] Site M0077. ***Ch—Chondrites*** **(black arrows);** ***Pa—Palaeophycus*** **(red arrows);** ***Pl—Planolites*** **(yellow arrows);** ***Zo—Zoophycos*** **(blue arrows); BI—bioturbation index (0–4).**

foraminifera zones Pα, P1a, and lower P1b); recent analysis indicated that this section is continuous for the first ~3 m.y. after the impact at Site M0077 (Lowery et al., 2018; Jones et al., 2019). The aim of this research was to investigate the initial diversification, evolution, restructuring, and stabilization of this macrobenthic community following the impact event.

EARLY PALEOCENE ICHNOASSEMBLAGE

Within the IODP/ICDP Site M0077 cores, the Danian section includes impactites of Unit 2 (617.3–713.8 m below seafloor [mbsf]), overlain by Unit 1G (616.6–617.3 mbsf), termed the Transitional Unit (TU), which in turn is overlain by Unit 1F (607.3–616.6 mbsf). We differentiated five parts (A to E) within this interval (Figs. 1 and 2; Fig. S2):

(A) Lower TU (below core 40R-1, 54 cm) shows preserved sedimentary structures (millimeter-scale parallel lamination) and absence of bioturbation (bioturbation index [BI] = 0).

(B) Upper TU (core 40R-1, 34–54 cm) shows *Planolites*, <4 mm in diameter, and *Chondrites*, <1 mm in diameter. Abundance is low (BI ~ 1).

(C) Lower 1Fc is 8 cm of the limestone overlying the TU (core 40R-1, 26–34 cm), and it shows an increase in size (*Planolites* 5–8 mm in diameter), abundance, and diversity of trace fossils, with the first record of *Palaeophycus* (4–8 mm in diameter), over a mottled background, and an increase in BI to 2.

(D) Lower 1Fb is the overlying 120 cm interval (core 39R-2 at 75 cm to core 40R-1 at 26 cm), and it shows a uniform trace fossil assemblage, with *Planolites*, *Chondrites*, and *Palaeophycus*, and no changes in size. From core 39R-3, 23 cm to Core 40R-1, 26 cm, *Planolites* is dominant, with local occurrence of *Chondrites* and *Palaeophycus*. From core 39R-2 at 75 cm to core 39R-3 at 23 cm, *Chondrites* (2–3 mm in diameter) is very abundant, together with *Planolites*. Moreover, an increase in the BI from low (1–2) to moderate/high (4) is observed, as well as a mottled background.

(E) Lower 1Fa, from 130 cm to 266 cm above the top of the TU (core 39R-1 at 66 cm to core 39R-2 at 75 cm), shows a change in the trace fossil assemblage with the appearance of well-developed *Zoophycos*, together with abundant *Chondrites* and *Planolites*, and a moderate/high BI (= 4). Ichnodiversity and abundance are maintained through the entire interval with only local *Palaeophycus*. A general increase in size is observed (*Chondrites* <4 mm, and *Palaeophycus* and *Planolites* ~10 mm in diameter).

EVOLUTION OF THE MACROBENTHIC TRACEMAKER COMMUNITY

The timing of postextinction recovery within the Chicxulub crater can be constrained based on an updated version of the age model constructed for IODP/ICDP Site M0077, according to data from lithology, biostratigraphy, ^{3}He measurements, Ir analyses, and Stoke's law calculations (Gulick et al., 2017, 2019; Morgan et al., 2017; Lowery et al., 2018; Goderis et al., 2019; Jones et al., 2019; see the Supplemental Material).

The trace fossil assemblages thus imply that initial recovery occurred within several years after the K-Pg transition (Lowery et al., 2018), before the final stage of atmospheric fallout of impact debris (Goderis et al., 2019), starting with scarce, small, *Planolites* (initial recovery; Figs. 3 and 4) after the absence of bioturbation. Immediately after, a first phase of diversification (diversification I; Figs. 3 and 4), and an increase in the abundance and size of burrows were detected, including the development of an initial community with *Planolites*, *Chondrites*, and *Palaeophycus*, as well as a shallow indeterminate infauna (mottled background). The tiering structure is dominated by the shallow and middle tiers, reflecting the activity of tracemakers just below the seafloor, and a few centimeters deep within the substrate. This diversification I phase extended to ~45 k.y. after the

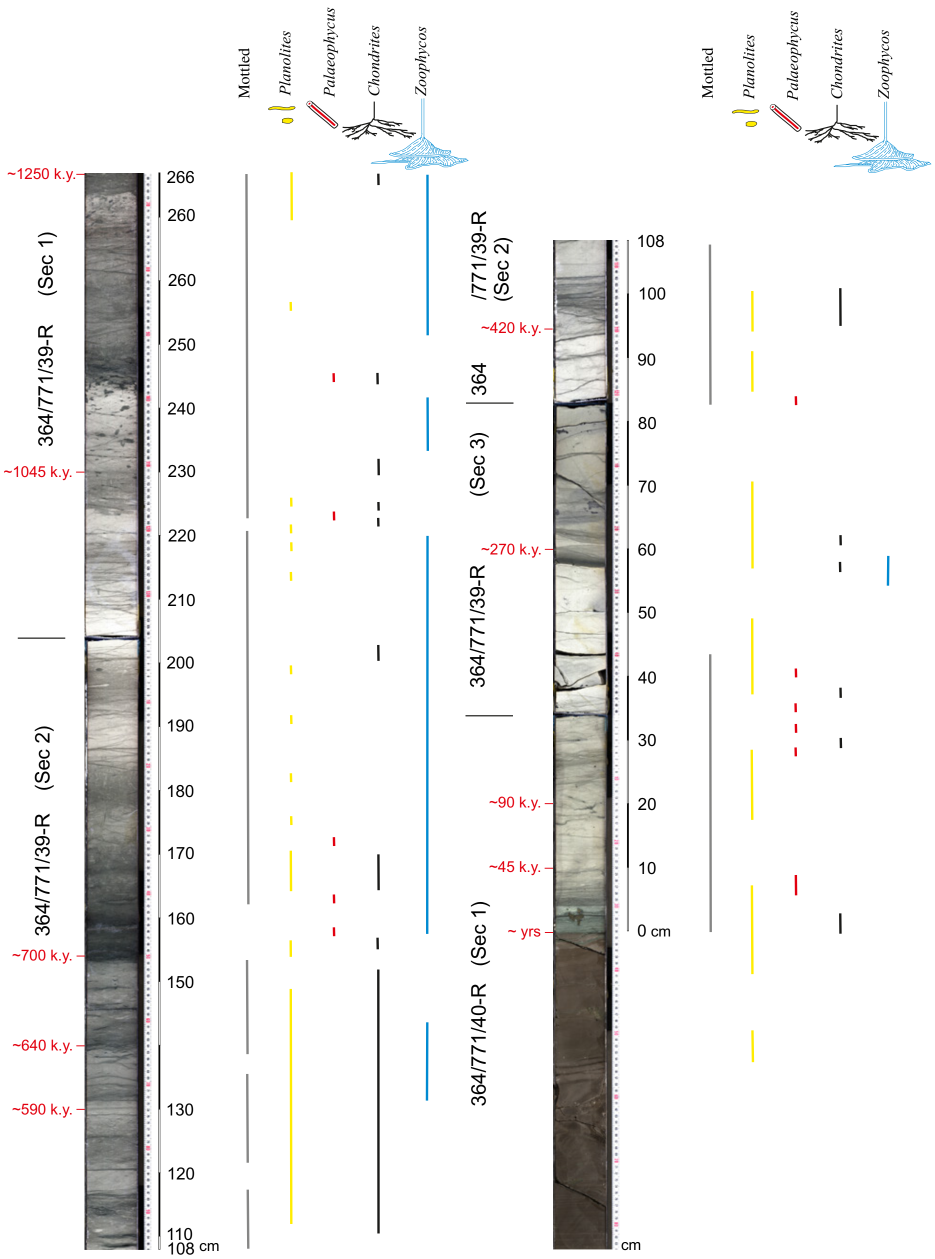

Figure 2. Distribution of ichnotaxa in cores from International Ocean Discovery Program (IODP)/International Continental Scientific Drilling Program (ICDP) Site M0077, showing distance from the top of the Transitional Unit and corresponding age.

K-Pg event (Figs. 2 and 3). Subsequently, the infaunal community stabilized, with changes only in relative abundance until ~640–700 k.y. into the Paleocene.

Minor fluctuations in environmental parameters (i.e., oxygen and nutrient availability) can cause changes in the relative abundance of tracemakers (*Planolites* vs. *Chondrites* as dominant ichnotaxon), such as those observed ~420 k.y. after the impact. An increase in abundance and size reveals the progressive rebuilding of a stable community structure. This prolonged phase of stabilization as followed by a new phase of diversification (diversification II; Figs. 3 and 4), with the appearance of *Zoophycos*, representing the recolonization of deep tiers, and showing activity down to some tens of centimeters within the substrate, during the interval ~640–700 k.y. This diversification marks the beginning of the highest diversity, abundance, and size of traces, with a community of *Zoophycos*, *Chondrites*, *Planolites*, and *Palaeophycus*. The dominance of *Zoophycos* reveals that the *Zoophycos* ichnofacies was completely established and maintained to the top of the studied interval (consolidation/dominance phase; Figs. 3 and 4), ~1.25 m.y. after the K-Pg event. Diversification II represents the full recovery, when a well-developed multitiered community is registered.

VARIABLE RESPONSE OF MACROBENTHIC TRACEMAKER COMMUNITY TO MASS EXTINCTIONS

Ichnological research on the "Big Five" mass extinctions has been conducted (e.g., Twitchett and Barras, 2004). However, ichnological analyses of the end-Ordovician, end-Devonian, and end-Triassic events are scarce (Twitchett and Barras, 2004), while the end-Permian (Luo et al., 2020) and the end-Cretaceous events (Labandeira et al., 2016) have been studied in detail.

The K-Pg macrobenthic tracemaker recovery can be compared with that from the end-Permian extinction (Permian-Triassic boundary [PTB]) based on Twitchett's recovery model (Twitchett, 2006). That model uses ichnologic characteristics similar to those presented in our study (key ichnotaxa, ichnodiversity, tiering structure, burrow diameter, or ichnofabric index), as a measure of relative recovery rates. Recovery stage 1 of the model, corresponding to the immediate extinction aftermath, shows the presence of rare, small, simple feeding structures (*Planolites*) of deposit feeders, as well as low ichnodiversity. From that, recovery stages 2, 3, and 4 show an increase in diversity, complexity (tiering), and diameter, with the final stage of recovery (stage 4) reflecting the return to pre-extinction ichnological features (Twitchett, 2006).

Although the overall recovery after the PTB was similar to that after the K-Pg event, the timing is very different. In the K-Pg recovery, the record of discrete, small, isolated *Planolites* (initial recovery) fits well with recovery stage 1, but at Chicxulub, this interval corresponds to the first few years after the extinction, whereas after the PTB, this recovery stage 1 lasts for, at most, one conodont zone (~10^5 yr; Twitchett et al., 2004). The first increase in diversity with *Planolites*, *Chondrites*, and *Palaeophycus* (diversification I, ~45 k.y. after the K-Pg event) can be correlated to the beginning of recovery stage 2 during the middle Early Triassic (Twitchett et al., 2004). Above that interval, the long period of stabilization of the tracemaker community (stabilization phase) corresponds to recovery stages 2 and 3 of the model. Finally, the appearance of *Zoophycos* (diversification II) and the establishment of a well-developed multitiered community (consolidation/dominance) correspond to recovery stage 4, and the complete restructuring of the macrobenthic tracemaker community.

The similarity of the recovery phases after the PTB and K-Pg mass extinction events is striking and suggests a similar response of the macrobenthic tracemaker community to paleoenvironmental changes. However, there is a significant difference in the pace of recovery. Most of the ichnological studies of the PTB extinction suggest that the recovery required several million years (Luo et al., 2020). During

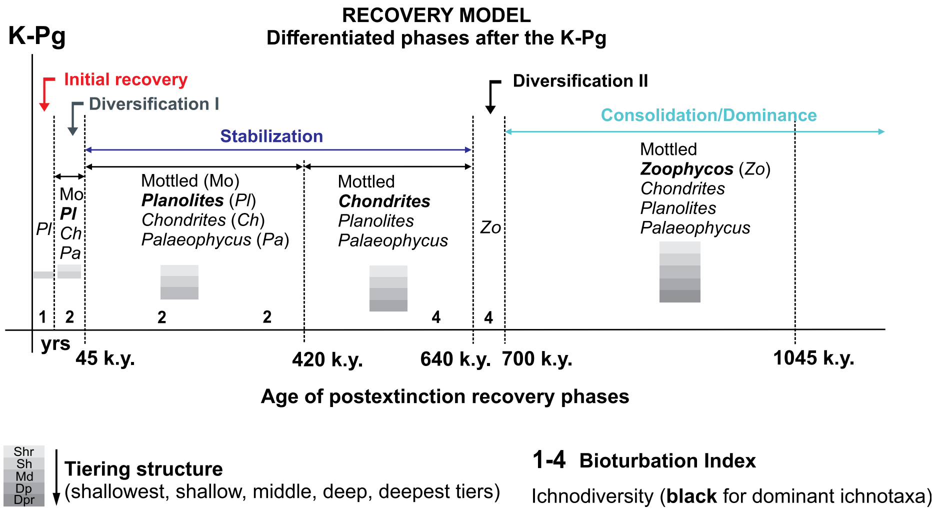

Figure 3. Proposed recovery model of macrobenthic tracemaker community after the Cretaceous-Paleogene (K-Pg) boundary impact with differentiated phases.

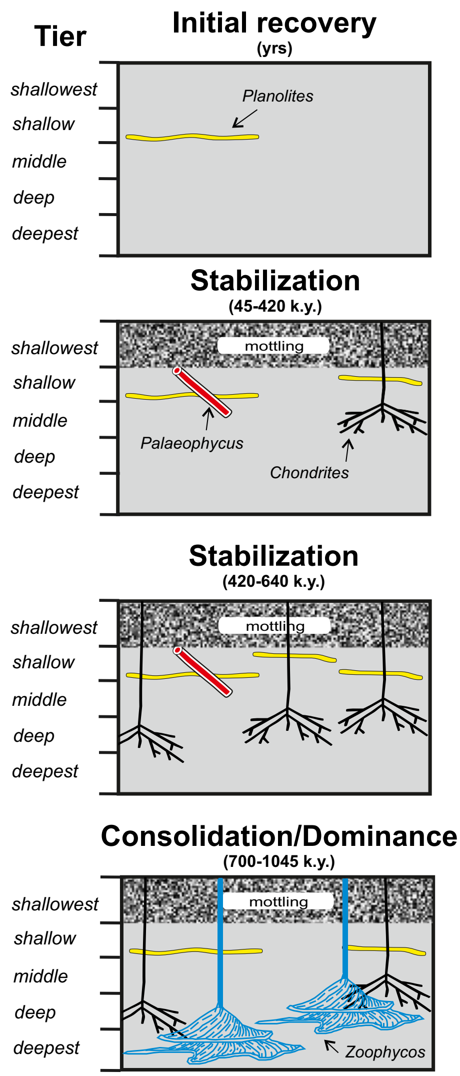

Figure 4. Tiering models according to differentiated phases in evolutionary pattern.

the early Paleogene at Chicxulub, full recovery was completed in ~700 k.y. This finding is remarkable considering that the Chicxulub crater was sterile immediately postimpact (Lowery et al., 2018), which suggests that the recovery of life was likely greatly aided by the ocean resurge and rapid infilling of the crater within the first day of the Cenozoic (Gulick et al., 2019). This comparatively fast recovery after the K-Pg impact could have been a result of several factors: (1) the severity of the end-Permian mass extinction, which was the greatest biotic crisis in Earth history (Luo et al., 2020); (2) relatively selective, minor impact for marine benthic communities in the K-Pg event, as compared to the severe benthic extinction during the PTB (Labandeira et al., 2016; Zhang et al., 2019); and (3) the persistence of oceanic anoxia associated with the PTB, which extended into the Early Triassic (Zhang et al., 2018), as compared to the ephemeral environmental perturbation at the K-Pg, characterized by rapid reestablishment of pre-impact conditions in distal sections (Sosa-Montes de Oca et al., 2020). Even at ground zero in the Chicxulub crater, trace element ratios and microfossils indicate elevated export productivity and the recovery of the food chain within months to thousands of years after the event (Lowery et al., 2018, 2020).

EXPORT PRODUCTIVITY AS A MAJOR FACTOR

Export productivity varied during the early Paleocene, according to microorganisms and geochemical proxies (Table S1; Hull et al., 2011; Jones et al., 2019), resulting in variations in the flux of organic matter to the seafloor. These variations presumably influenced the recovery of the macrobenthic tracemaker community. In a well-oxygenated environment in an upper/middle bathyal zone (Lowery et al., 2018), nutrient availability is the main limiting factor for tracemakers. Export productivity in the Chicxulub crater was high for the first 300 k.y. after the K-Pg event and then decreased abruptly (Table S1; Lowery et al., 2020). After that time, export productivity slowly declined between 300 and 1000 k.y. postimpact, with a second peak in export production occurring ~800 k.y. postimpact, and then it remained low through the next ~1 m.y. (Table S1; Lowery et al., 2020). The first 300 k.y. with high export productivity could have facilitated the initial diversification and stabilization of the community (*Planolites*, *Chondrites*, and *Palaeophycus*, and shallow indeterminate infauna). This record suggests high rates of organic matter transport to the sediment and availability of nutrients at or just below the seafloor to a few centimeters deep within the substrate (Rodríguez-Tovar and Uchman, 2004, 2006). The subsequent decline in export productivity could have induced the change in the relative abundance between tracemakers (*Planolites* versus *Chondrites*) observed at ~420 k.y. postimpact. Finally, the appearance of *Zoophycos* ~640–700 k.y. after the K-Pg boundary, during the diversification II phase, could have been associated with relatively low sedimentation rate and low organic matter fluxes, where organic matter at the sediment surface may have been rapidly oxidized. Under these conditions, deep-tier structures are produced by organisms such as *Zoophycos* tracemakers, which are able to store organic matter deeper in the sediment (Löwemark, 2015).

CONCLUSIONS

Ichnological analysis supports the rapid complete recovery of the macrobenthic tracemaker community after the end-Cretaceous (K-Pg) mass extinction event within the Chicxulub impact crater. Tracemakers first appeared in the crater within a few years of the impact, even before the atmospheric fallout of impact debris, and a mature, multitiered macrobenthic community was established ~700 k.y. after the impact. Comparison with the end-Permian extinction reveals similarities in the structure and progression of recovery, although the K-Pg recovery was significantly faster. This rapid recovery may have been related to the shorter duration of paleoenvironmental changes related to the K-Pg event and the different effects of the two events on benthic communities. One of the primary lingering effects of the Chicxulub impact was a global shift in export productivity, and thus changes in ichnodiversity and abundance of trace fossils responded primarily to variations in the flux of organic matter to the seafloor during the early Paleocene.

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