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Extinction trajectories of benthic organisms across the Triassic–Jurassic boundary

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Abstract

We analysed diversity and abundance patterns of benthic organisms across the Triassic–Jurassic (T-J) boundary based on the Paleobiology Database (PBDB), which compiles palaeontological collection data on a global scale. While Sepkoski's [Sepkoski, J.J. Jr., 2002. A compendium of fossil marine animal genera. Bulletins of American Paleontology 363, 1–563] compendium on the stratigraphic ranges of marine animal genera suggests that the dominant macrobenthic groups of the Late Triassic experienced significant extinctions prior to the T-J boundary, a significant end-Triassic extinction peak is evident from PBDB's data. This Rhaetian extinction peak is found in both an analysis of the raw data of stratigraphic ranges and a sample-standardized analysis of occurrence data; 41% of all mesobenthic and macrobenthic genera crossing the Norian–Rhaetian boundary became extinct within the Rhaetian. Although this rate suffices to characterize the end-Triassic extinction as a true mass extinction against a Middle Triassic to Middle Jurassic background, significantly reduced Rhaetian origination rates add to the strong diversity depletion in the earliest Jurassic.

As for other mass extinctions, evidence for selective extinction is meagre when the analysis is limited to the boundary interval alone and when focused on taxonomic and ecological characteristics of individual genera. When taxa are separated by environmental preferences, however, several determinants of extinction risk become evident, suggesting that reef dwellers had a significantly higher extinction risk than level-bottom dwellers, taxa with an inshore preference were more strongly affected than offshore taxa, taxa preferring carbonate substrates were more strongly hit than taxa preferring siliciclastic substrates and taxa preferentially inhabiting low latitudes had higher extinction rates than taxa more common at intermediate and high latitudes. Much of this selectivity is not independent and also seen in the intervals of background extinctions suggesting that the end-Triassic mass extinction represents an intensification of background extinctions but not a qualitatively different macroevolutionary regime. One possible exception is related to preferences for depositional environments suggesting a selective Rhaetian extinction in reefs and inshore settings.

Keywords: Triassic; Jurassic; Rhaetian; Mass extinctions; Reefs; Level-bottom communities; Selectivity

1. Introduction

The end-Triassic extinction remains the least understood of the 'big five' Phanerozoic extinction events, which have been detected based on statistical analyses of the stratigraphic ranges of marine taxa (Raup and Sepkoski, 1982). Although several hypotheses on the cause of the end-Triassic extinction are currently discussed (Ward et al., 2001; Beerling, 2002; Olsen et al., 2002; Pálfy, 2003; Marzoli et al., 2004; Tanner et al., 2004; Galli et al., 2005), the biotic patterns across the boundary remain poorly documented and explored. Our perception of global

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extinction patterns across this boundary still relies heavily on Sepkoski's compendia listing the stratigraphic ranges of marine taxa (Sepkoski, 1992, 2002). A recent comparative approach, also based on Sepkoski's data, sheds some new light on the end-Triassic mass extinction in that it clearly separated the effects of extinction and origination (Bambach et al., 2004) and found that the end-Triassic was characterized by both elevated extinction rates and depleted origination rates. Still lacking in this approach was a separation of the Norian and Rhaetian stages and, most importantly, a quantitative consideration of heterogeneities in the palaeontological record. Bambach et al. (2004), and more qualitative studies (Hallam, 2002; Tanner et al., 2004), have challenged the end-Triassic extinction as a true mass extinction event. This refers to both the timing and the magnitude of the extinction.

Most analyses of benthic marine extinction patterns focus on Europe where a wealth of data are available, especially from the Alpine region (McRoberts, 1994; McRoberts and Newton, 1995; Hallam, 2002). Although detailed sections, some of them currently discussed as potential stratotype sections, are available outside of Europe, no global analysis on the marine benthos through the Triassic–Jurassic (T-J) boundary interval has been performed so far (but see McRoberts, 2001 for a global analysis of bivalves), and, even more importantly, all previous analyses using global data sets rely on raw data without standardizing for heterogeneous preservation and sampling intensity.

Here we focus on extinction trajectories of macrobenthic and mesobenthic organisms and compare these with ecological changes in benthic ecosystems. Our primary goals are (1) to assess the magnitude and significance of the end-Triassic extinction in benthic organisms; (2) to test for extinction selectivity by ecological traits and environmental preferences (especially reefs versus level-bottom ecosystems); and (3) to contrast trajectories of extinction intensity and ecological changes. Although our results cannot assess the timing of the extinction within the Rhaetian, we also discuss the consequences of our results for potential causes of the end-Triassic extinction.

2. Databases and methods

2.1. Studied groups of organisms

Our analyses focus on benthic invertebrate taxa and exclude nektonic and planktonic organisms and all microfossils. However, mesobenthic organisms such as calcareous algae, often analyzed in thin sections, are included. Core groups that are analyzed in some detail include sponges, corals, bivalves, gastropods and brachiopods.

2.2. Database

The Paleobiology Database (PBDB; http://paleodb.org) was our primary data source for the evaluation of sample-standardized extinction rates and the assessment of taxon abundances. PBDB compiles palaeontological collection data of the entire Phanerozoic at a global scale. The PBDB data set used for the analyses encompasses data from the Middle Triassic to Early Cretaceous (Anisian to Hauterivian stages, ca. 245–130 Ma). The raw data have been downloaded on July 25, 2005. The download used the default settings with the exception that only data of the marine invertebrate working group were used and generic occurrences qualified as "aff." and in quotation marks were omitted. The taxonomic data were corrected for obvious typing errors of genera and revised by following published opinions and by checking up-to-date synonymy lists in the literature. Most noteworthy for revision of coral data are the papers of Beauvais (1986), Roniewicz (1989), Stanley and Whalen (1989) and Roniewicz and Michalik (2002). Data of thalamid sponges were revised following Senowbari-Daryan (1990), while synonymization of Triassic bivalves was largely based on recent monographs (e.g., Hautmann, 2001a,b; Waller and Stanley, 2005). Jurassic bivalve data were vetted based on the personal taxonomic experience of one of the authors (MA). However, even the strongest efforts cannot eliminate all the taxonomic errors, and there always is subjectivity in taxonomic assignments. Therefore, we have performed a cross-check of our raw generic ranges with Sepkoski's (2002) compendium. If PBDB's first or last appearances were off by more than 20 million years from the compendium data, or if genera crossing the T-J boundary were not listed as boundary-crossing taxa in the compendium, we carefully checked the primary collection records and, if possible, the original reference of the collection. We deleted taxonomic occurrences that could not be verified from the file prior to performing analyses on biodiversity dynamics. However, we maintained these occurrences for the assessment of ecological traits on the assumption that a general ecomorphotype had been identified. Altogether, some 1000 species have been assigned to different genera and nearly 1000 occurrences were omitted from the raw file prior to analysis.

Although we performed thorough taxonomic reassignments in PBDB data, the taxonomy is still based on a typological approach. Phylogenetic studies, e.g., on T-J corals have been attempted (Roniewicz and Morycowa, 1989; Roniewicz and Stolarski, 1999), but are limited to major clades. Phylogenetic analyses at the species level are not yet available for the groups under study.

The final data set used for analyses comprises 4790 collections (faunal lists) and 37,023 taxonomic occurrences