

Invited Review Article

Paleoecological Response of Corals to the End-Triassic Mass Extinction: An Integrational Analysis

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ABSTRACT: The end-Triassic (also Triassic-Jurassic) mass extinction severely affected life on planet Earth 200 million years ago. Paleoclimate change triggered by the volcanic eruptions of the Central Atlantic Magmatic Province (CAMP) caused a great loss of marine biodiversity, among which 96% coral genera were lost. However, there is precious little detail on the paleoecology and growth forms lost between the latest Triassic extinction and the Early Jurassic recovery. Here a new pilot study was conducted by analyzing corallite integration levels among corals from the latest Triassic and Early Jurassic times. Integration levels in corals from the Late Triassic and Early Jurassic were determined through both the Paleobiology Database as well as from a comprehensive museum collection of fossil corals. Results suggest that in addition to a major loss of diversity following the end-Triassic mass extinction, there also was a significant loss of highly integrated corals as clearly evidenced by the coral data from the Early Jurassic. This confirms our hypothesis of paleoecological selectivity for corals following the end-Triassic mass extinction. This study highlights the importance of assigning simple to advanced paleoecological characters with integration levels, which opens a useful approach to understanding of mass extinction and the dynamics of the recovery.

KEY WORDS: coral loss, integration level, end-Triassic mass extinction, paleoecology

0 INTRODUCTION

Roughly 200 million years ago the end-Triassic or Triassic-Jurassic mass extinction severely affected life on planet Earth. It ranks among the five biggest extinction events in the Phanerozoic history of life and the resulting biotic changes are indelibly etched into the geologic record. The end-Triassic extinction event severely affected both terrestrial and marine environments with major losses of diversity among most of the dominant organisms. In the marine environment this included reef-building corals and sponges. Volcanic eruptions of the Central Atlantic Magmatic Province (CAMP) at the end of the Triassic, produced prodigious amounts of greenhouse gases (Marzoli et al., 1999). As indicated by physical and geochemical evidence (Cohen et al., 2002), CAMP volcanism appears to have coincided closely with the end-Triassic mass extinction (Nomade et al., 2007; Bertrand, 2006) which eliminated over 75 percent of species. Many possible kill mechanisms have been difficult to unravel because of the differential effects of the extinction on life of the end-Triassic (Lucas and Tanner, 2008; Tanner et al., 2004). It is clear that the extensive CAMP volcanism had profoundly negative effects upon the whole planet for both terrestrial and marine life. Details of the Early Jurassic recovery are emerging and the timing based on

study of key boundary sections is greatly refined. This led to the conclusion that following the end-Triassic mass extinction, the terrestrial ecosystem was recovering while the marine ecosystem continued to be disturbed (Lindström et al., 2017).

Corals were major reef builders of the latest Triassic and reefs were widespread and corals were diverse during the Triassic (Flügel, 2002). Following the CAMP scenario, the marine environment perturbations of the Late Triassic included sea-level and climate change as well as severe marine anoxia associated with the disruption of the carbon cycle and major acidification of the seawater (Hautmann et al., 2008). Ocean acidification and a postulated drop in ocean pH severely affected thriving corals and among other things, decreased their ability to form skeletons (Greene et al., 2012; Martindale et al., 2012). Because of ocean acidification, the marine environment and plankton experienced a severe biocalcification shock at the end of the Triassic (van de Schootbrugge et al., 2007). Corals, diverse and important in reefs, were especially hard hit by the extinction and suffered far greater extinction losses relative to other invertebrates. Unlike calcite-secreting organisms, corals of the latest Triassic were at a distinct disadvantage because, like living species, they likely had poor physiological control over biocalcification. The onset of ocean acidification at the end of the Triassic, reduced physiological control of calcification with respect to aragonite saturation and along with other factors, might account for their high extinction rate (Hautmann, 2012, 2008; Kiessling and Simpson, 2011).

Past analyses of the T/J extinction patterns confirmed a previously suspected depletion of diversity within the Rhaetian or last stage of the Triassic, followed by a much greater end-

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Triassic extinction with preferentially higher selectivity among reef-building and reef-dwelling sponge and coral taxa in the tropical Tethys (Hautmann, 2012; Kiessling et al., 2007). Although there are good data for the extinction response among other groups such as bivalve taxa (Damborenea et al., 2017), the effects of extinction on corals are not well known.

Early estimates of the effects of the end-Triassic extinction confirm that the number of coral taxa lost was very high. Of 321 Triassic coral species tabulated by Reidel (1991) only 14 were found in the Early Jurassic and this represents less than 1% survival (Stanley and Beauvais, 1994). Tabulations by Flügel (2002) indicated an extinction of 96% of coral genera but the data may have been biased by sampling, standardization of statistics and other criteria (Kiessling et al., 2007) and may not have been this high. Coral extinction at the T/J was indeed high but the start of the Early Jurassic recovery began quickly and commenced during Hettangian time (Lathuilière and Marchal, 2009). Overall coral diversity was low and there is an absence of large-scale reefs but scattered small coral bioconstructions are known in the western Tethys and Asia during that time (Melnikova and Roniewicz, 2017; Gretz et al., 2013; Kiessling et al., 2009). The recovery fauna was mostly composed of relic holdover Triassic corals as well as some newly evolved taxa (Melnikova and Roniewicz, 2012).

While data is available about diversity losses of coral taxa, there is precious little detail on the paleoecology and growth forms lost between the latest Triassic extinction and the Early Jurassic recovery. Here we present a new pilot study, analyzing corallite integration levels among corals from the latest Triassic and Early Jurassic times. We test the hypothesis that the corals selected for extinction were paleoecologic specialists and that, as discussed below, these can be assessed by study of integration levels.

1 PREVIOUS WORK

Corals are diverse, modular organisms and the integration of their units are difficult to quantify. Wood (1999) discussed modularity to suggest that the ability to grow, extend and cooperate for mutual success is directly related to the degree of relative dependence of individuals within a colony. For fossil corals this is assessed by corallite integration. Coral integration is defined as the degree of sharing and cooperation between the individual polyps within a colony and ultimately is expressed by the arrangement of corallites and the complexity of the corallum. Increasing levels of integration produce specializations and in competitive environments like reefs, bestow distinct adaptive advantages to colonial corals in terms of their feeding cooperation, reproduction, growth and ecological success.

Corallite integration level and coloniality were first investigated by Coates and Oliver (1973). These authors established and quantified integration levels among Paleozoic to modern corals. Coates and Jackson (1987) ranked corallite integration from high to low based upon data derived from published coral monographs. This pioneering work revealed general trends of increasing levels of integration through time. Occurrence of relatively high levels of coral integration equated with larger corallite size, paleoecology and major episodes of reef-building. Among modern corals high integration levels relate to fitness

and resistance to stress, especially bleaching (Swain et al., 2018). Study of coral integration levels in geologic time may help better understand the evolution of coloniality and the adaptive success of corals.

In addition to the degree of high levels of integration, many corals in tropical and subtropical settings, especially those that build reefs, also have photosymbiosis with one-celled dinoflagellates (zooxanthellae) living in their tissues. This greatly benefits corals by increased nutrition and growth. Establishing photosymbiosis in the fossil record is somewhat problematical because the symbionts do not preserve. Lipps and Stanley (2016) summarized multiple criteria among fossil organisms to help assess the former presence of photosymbiosis and they followed trends for various organisms through geologic time. The success of shallow-water corals, and especially reef builders today is closely linked with their one-celled endosymbionts (*Symbiodinium*).

It was suggested that among modern and ancient corals, high integration levels correlate with photosymbiosis (Coates and Oliver, 1987; Barbeitos et al., 2010). What about the early scleractinians of the Triassic? Assessments of the photosymbiotic potential of Upper Triassic corals provided evidence that they were mostly if not entirely photosymbiotic (Stanley and Swart, 1995). This conclusion on the photosymbiotic paleoecology of Upper Triassic corals more recently was reached by Stanley and Lipps (2011), Stanley (2006), Frankowiak et al. (2016) and Tornabene et al. (2017). With respect to integration levels, it is unclear how the end-Triassic mass extinction and subsequent recovery in the Jurassic related to levels of integration among corals.

2 METHODS

In order to assess and compare the integration level of coral before and after the end-Triassic mass extinction, we determined the integration levels in corals from the Late Triassic and after the mass extinction in the Early Jurassic. Our methodology consisted of analyzing integration states from a coral database as well as from a comprehensive museum collection of fossil corals. We established integration levels for corals, assigning those numbers of increasingly higher states, ranging from 1 to 10.

The lowest integration state, 1, categorized solitary forms. For colonial corals dendroid, phaceloid and all uniserial branching types are the simplest and all were assigned number 2. More complex multiserial branching corals were given an integration number of 3. Cerioid (number 5) had corallites separated by a distinct wall. These and other examples are defined below and explained in Table 1. Illustrated examples of actual corals are given in Fig. 1.

2.1 Coral Integration Definitions

(1) Solitary: coral growth form in which each corallite is independent and thus not colonial.

(2) Pseudo-colonial: simple coral in which some corallites are connected to another but there is no branching.

(3) Uniserial branching: coral colony form in which corallites branch and individual corallites are separated by void space. This includes both dendroid and phaceloid forms (Faure et al., 2007).

(4) Multiserial branching: coral colony form in which coral-

lites branch and cerioid-like corallites cover surface of each branch.

(5) Cerioid: coral colony form in which corallites are juxtaposed and share a common wall. There is no coenosteum. This includes plocoid and kuhnasteroid forms (Faure et al., 2007).

(6) Cerio-meandroid: coral colony form in which corallites form short series without wall separation, and each short series is separated by a shared wall. There may be instances of individual corallites separated by walls in addition to series of corallites in a single specimen.

(7) Astreoid: coral colony form in which corallites are juxtaposed without a wall separating one corallite from its neighbor so septa do not continue from one corallite to another (Cairns et al., 2010).

(8) Thamnasteroid: coral colony form in which septa of corallites continue from one corallite to the next (Cairns et al., 2010).

(9) Pseudo-meandroid: coral colony form in which the corallites are arranged in short, multiple series, falsely resembling true meandroid types.

(10) Meandroid: coral colony form in which the corallites are arranged in multiples of series consisting of valleys with ridges separating adjacent valleys. These series may vary in length within a single specimen.

2.2 Database Analysis PBDB

We obtained scleractinian coral species from Rhaetian, Hettangian, and Sinemurian stages from the Paleobiology Database (<https://paleobiodb.org/>). Results are given in Fig. 2. Using this list, we assigned each species one or more integration types based on the published descriptions. To each type we assigned an integration number as explained above. If a given coral matched more than one integration type, we based the number on the most common integration type observed.

2.3 Collection Analysis

To compare the database results with actual examples, we also made integration assignments to Rhaetian, Hettangian, and Sinemurian corals housed in the collections at the University of Montana Paleontology Center. Here large collections of Early Mesozoic corals are housed, including an extensive collection from the Zlambach Formation in the Alps (<http://hs.umt.edu/paleo/>). Through direct observation of these specimens, we assigned an integration type and number to each. Results are given in Fig. 3.

The Hettangian follows directly after the T/J mass extinc-

tion and corals of this age are extremely rare. Also, it is in some cases stratigraphically difficult to distinguish Hettangian from Sinemurian stages. To gain a better representation, we lumped both Hettangian and Sinemurian corals. The data are labeled by museum number, taxon (if available), integration type, integration number, locality, locality number, locality age, and formation. In this study there were 282 identifiable specimens from the Rhaetian, and 139 identifiable specimens from the Hettangian/Sinemurian. Hettangian/Sinemurian coral specimens of the Jurassic originated from New York Canyon in west-central Nevada and come from the Sunrise Formation (Hodges and Stanley, 2015); the Sierra de Santa Rosa Formation at Sierra de Santa Rosa, northwestern Sonora, Mexico (González-León et al., 2017); the Telkwa Formation, British Columbia, Canada (Stanley and McRoberts, 1993) and a Hettangian coral site from southern France (Kiessling et al., 2011).

2.4 Publication Analysis

We also assessed integration types from published illustrations of Upper Triassic corals by Roniewicz (1996) in her large monograph on Upper Triassic corals of the Zlambach Formation in the Northern Calcareous Alps, Austria. This is a more up-to-date representation of an older monograph by Frech (1890). A chapter on corals from Tajikistan (Melnikova, 2001) was used to supplement for corals not found in the Roniewicz

Table 1 Integration number given to each coral in our assessments (Categories are explained in the text)

Integration type	Integration number
Solitary	1
Pseudo-colonial	2
Dendroid	3
Phaceloid	3
Uniserial Branching	3
Multiserial	4
Cerioid	5
Cerio-meandroid	6
Astreoid	7
Thamnasteroid	8
Pseudo-meandroid	9
Meandroid	10

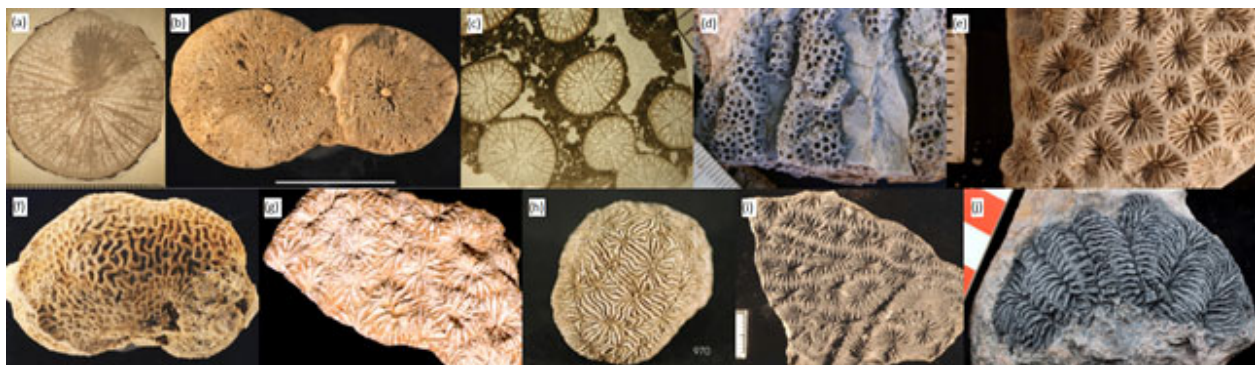


Figure 1. Illustrated examples of actual corals contained in coral integration definitions. (a) Solitary; (b) pseudo-colonial; (c) uniserial branching; (d) multiserial branching; (e) cerioid; (f) cerio-meandroid; (g) asteroid; (h) thamnasteroid; (i) pseudo-meandroid; (j) meandroid.

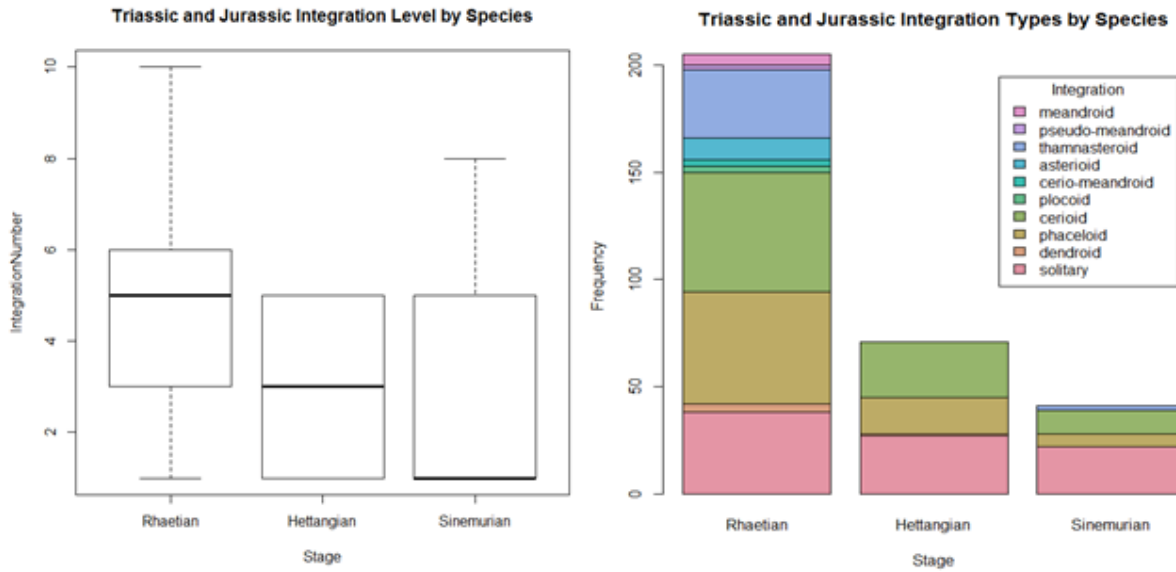


Figure 2. Left: trend of coral integration levels from Late Triassic to Early Jurassic based on species data in Paleobiology Database; right: detailed distribution of integration types that each species belongs to from Late Triassic to Early Jurassic.

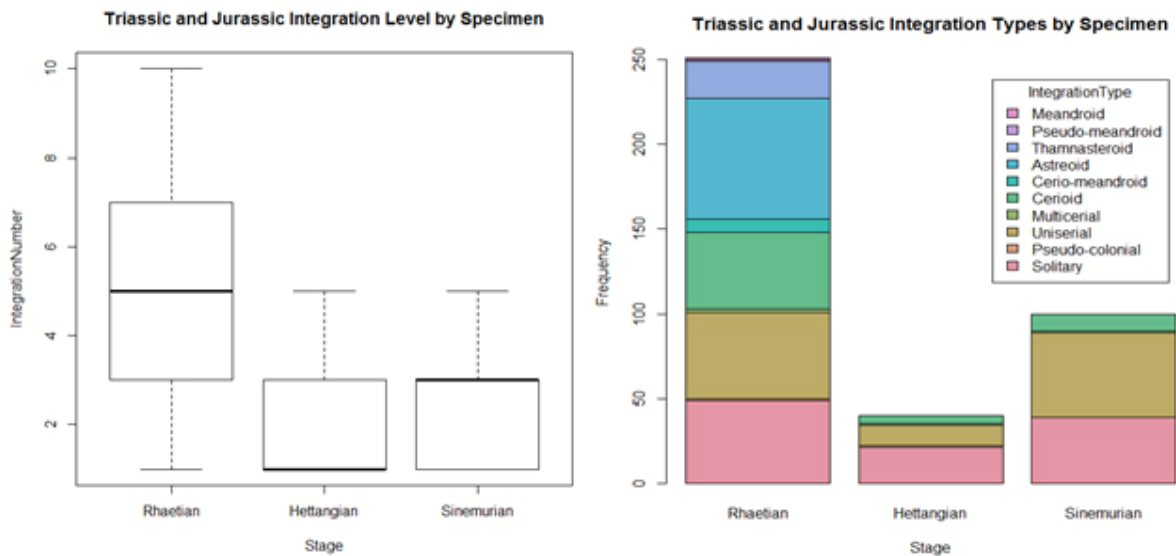


Figure 3. Left: trend of coral integration levels from Late Triassic to Early Jurassic based on specimen collections; right: detailed distribution of integration types that each specimen belongs to from Late Triassic to Early Jurassic.

monograph. In addition, we used corals illustrated in published papers (Caruthers and Stanley, 2008; Roniewicz, 1996, 1989; Squires, 1956; Smith, 1927). These assessments were compared with actual specimens in the UMPC collections in order to check for any bias.

This also was done for the Early Jurassic corals using published papers (Melnikova and Roniewicz, 2017; Gretz et al., 2013; Melnikova and Roniewicz, 2012; Kiessling et al., 2009; Lathulière and Marchal, 2009; Stolarski and Russo, 2002; Negus, 1991, 1983; Roniewicz and Morycowa, 1989) and the monograph by Duncan (1884). Once all the assessments were made, the average of each integration level within each time frame was measured and then compared. In addition to finding

the average of each integration level, we performed an analysis of diversity of the integration levels. This was done after all the corals have been double checked for accuracy.

Using the program *R* and the package *R commander* (R_{cmdr}), we analyzed the data from the taxon list and the specimen list. We used the linear model Integration Number~Stage and Integration Number~Period for each set of data. We also used One-way ANOVA to compare the variance of integration types within and between each stage. Finally, we compared the models Integration Number~Stage (Rhaetian, Hettangian, and Sinemurian) to Integration Number~Period (Triassic and Jurassic).

3 RESULTS

As discussed below we report results from two analyses: those from the PBDB and those from the collections.

3.1 PBDB Results

The analysis of the Paleobiology Database showed greater diversity of integration types among the corals of the Rhaetian stage (Late Triassic) than those of the Upper Jurassic Hettangian and Sinemurian stages (Fig. 2). In addition, Rhaetian corals yielded much higher levels of integration, including examples of every type including the meandroid category. The mean integration number for Rhaetian coral species was 4.5, the mean integration of the Hettangian coral species was 3.0, and the mean of the Sinemurian coral species was 2.7.

We found that the end-Triassic mass extinction had a significant effect on the integration level of the coral species. Through Analysis of Variance (ANOVA) model of Integration Number~Stage we found a p -value of 0.000 000 070 9, and the ANOVA model Integration Number~Period had a p -value of 0.000 000 011 1. This shows that the Jurassic coral species were significantly less integrated than the Triassic coral species, even into the Sinemurian stage. Late Triassic (Rhaetian) coral species included everything from solitary to highly integrated meandroid corals, but earliest Jurassic (Hettangian) featured corals with lower integration (nothing higher than cerioid). Sinemurian corals are slightly more integrated, yielding only four taxa with thamnasteroid-level integration.

3.2 Specimen-Level Data from UMPC Collection

Among the specimens analyzed from the UMPC collection (UMPC), we again found a much greater diversity in the Rhaetian than in the Hettangian and Sinemurian, and higher levels of integration (Fig. 3). The mean integration number of the Rhaetian coral species was 4.7, while the mean integration of the Hettangian and Sinemurian taxa were 2.2 and 2.4, respectively.

Among the specimens observed from the UMPC, we again confirmed our hypothesis about the selectivity of the end-Triassic extinction on the integration levels of corals. Both the ANOVA model Integration Number~Stage and Integration Number~Period have p -values of $<2e-16$. A comparison of the two models has a p -value of 0.563 1, showing that there is no significant difference between the two models. Again, the Early Jurassic corals were significantly less integrated than those of the Triassic. While the Triassic specimens yielded corals spanning every integration type, the Early Jurassic specimens were more restricted, never attaining an integration level over 5 (cerioid).

4 DISCUSSION AND CONCLUSION

Our results expand upon that of Coates and Oliver (1973). It was improved by delineating more integration states, by incorporating Early Jurassic corals and by using both collection-based and publication-based data. Our results and findings suggest that in addition to a major loss of diversity, following the end-Triassic mass extinction, there also was a significant loss of highly integrated corals as clearly evidenced by the coral data from the Early Jurassic. This confirms our hypothesis of paleoecological selectivity for corals following the

end-Triassic mass extinction. The pre-extinction corals of the Late Triassic were diverse and highly integrated and many were reef-building and assumed to have been photosymbiotic. Such highly integrated and specialized corals were apparently unable to survive the end-Triassic mass extinction which as previously mentioned, was characterized by ocean acidification, anoxia and other causes—all quite inimical to shallow-water reef species.

The results of the analysis of integration levels also support previous conclusions that these zooxanthellate (photosymbiotic) corals were unable to adapt to conditions of the mass extinction and that some of the post-extinction survivors in the Early Jurassic, most of which appear a zooxanthellate-like (nonphotosymbiotic), survived.

There are very few up-to-date taxonomic studies of diversity trends among Early Jurassic, post-extinction corals. The best summary of extinction and recovery is that of Lathuilière and Marchal (2009). These authors suggested that the recovery was underway very soon after the mass extinction. A large number of surviving Jurassic corals were Triassic holdovers based on our integration study of publications from the Americas, England, Scotland, France and central Asia. The Early Jurassic corals were either solitary forms (Melnikova and Roniewicz, 2017; Hodges and Stanley, 2015) or a mixture of solitary and lower integrated forms (Gretz et al., 2013; Kiessling et al., 2009; Wells, 1956; Duncan, 1884). The earliest Jurassic colonial corals were branching uniserial forms (dendroid and phaceloid) with somecerioid types while higher integrated corals notably are absent. A recent study of Early Jurassic corals from Argentina (Echevarría et al., 2017) revealed a two-step process of recovery, starting with low morphologic diversity in the Hettangian (only a few solitary corals recorded) and increases in the diversity in Sinemurian time. A sharp increase in diversity by Early Pliensbachian time was followed by evolution of more complex colonial forms with taxa appearing increasingly more zooxanthellae-like.

Understanding how corals responded to rapid climate change during the end-Triassic mass extinction is of paramount value in understanding what is happening to corals and reefs today. Adverse changes in the marine environment, such as rise in greenhouse gases, ocean acidification and global climate, are among the key factors degrading corals and reefs. Under the scenario of predicted changes in the marine environment, corals are anticipated to experience massive global bleaching with loss of algal symbionts and acidification of seawater, leading to destruction of both reefs and photosymbiotic corals (Stanley and van de Schootbrugge, 2018). It is predicted that by the end of 2050, all shallow-water corals will become extinct (Burke et al., 2011). Although humans are clearly implicated in the marine crisis through overfishing and nitrification of seawater, the main underlying problem is rapid climate change. From the results gathered here in our analysis of fossil counterparts, it can be predicted that the most diverse corals with higher integration levels and photosymbiosis (i.e., zooxanthellate taxa) will die out first and relative to nonsymbiotic (ahermatypic) taxa, will be less likely to recover.

In an ecologically close relationship, photosymbiotic corals (zooxanthellate) cannot live without their dinoflagellate

symbionts. With regard to feeding and other aspects of their ecology, living and fossil azooxanthellate (non-photosymbiotic) corals are generalists. Unlike their photosymbiotic counterparts, they lack symbionts for growth and supplementation of nutrition but can live in deep and cold water up to high latitudes (Stanley and Cairns, 1988). As outlined by Coates and Jackson (1987) such corals exhibit low levels of corallite integration (solitary, branching and cerioid). Clearly lower integrated corals without photosymbionts have better potential for survival during mass extinction. Of interest are findings from molecular research on living corals suggest that coloniality and symbiosis repeatedly were acquired and lost during the history of the Scleractinia (Barbeitos et al., 2010). Survival in deep water or at high paleolatitudes is a possibility and could be an evolutionary survival mechanism. It would be interesting to test this idea on corals at other mass extinction events. Talent (1988) proposed a correlation between photosymbiosis, extinction and episodes of reef building during the Phanerozoic. This was supported and reiterated by Stanley and Lipps (2011) who discussed connections between reef collapse and loss of photosymbiosis among highly integrated corals.

Investigations of extinction and recovery at key extinction boundaries traditionally assess taxonomic diversity. Assigning simple to advanced paleoecological characters with integration levels, opens an useful approach to understanding of mass extinction and the dynamics of the recovery. It also offers insights into the causes of the extinction. It is possible that non-coral fossil groups similarly could be ranked by complexity and lend themselves to this type of analysis.

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