Coral reef bioerosion in times of crises – the Late Triassic/Early Jurassic example

M. Bertling

ABSTRACT

A study across the major extinction phase of scleractinians during the Late Triassic/Early Jurassic was performed. Samples from seven localities in Austria, Morocco and Iran were quantitatively evaluated for macroborings. Each locality represents a turbid or clear-water environment before and after the 5 million years of crisis. Norian reefs suffered almost no bioerosion in clear water but in a turbid setting, they were moderately bored with “worms” dominating over bivalves and cirripeds. Late Rhaetian reefs independently of the environment were slightly bored by the same array of borers. In the Plünsbachian, “worms” still dominated over bivalves and cirripeds, again independent of the facies. The pattern of coral reef macroboring hence remained essentially unchanged across the major end-Triassic extinction phase of corals. There is good evidence for joint evolution of coral borers and their substrate. Borers did not facilitate the Late Triassic reef decline but they did respond to it.

Keywords Bioerosion, Jurassic, Triassic, Reefs, Corals

Introduction

Is bioerosion responsible for the demise of modern reefs, or are high rates of macroboring (e.g. Goreau and Hartman 1963, Acker and Risk 1985) just an epiphenomenon of reduced coral vitality? The term bioerosion comprises processes by which organisms destroy hard substrates (Neumann 1966); its significance for the structure and function of modern reefs is generally recognized. The introductory question asked by some conservation biologists might be answered by investigating previous reef crises in Earth history; the fossil record should have preserved both the pre- and post-extinction situation. The Late Triassic/Early Jurassic scleractinian crisis was selected as an example here because several reefs of this age have been documented in the literature (see “Materials and Methods”). They had not been studied in terms of bioerosion, however.

Reef bioerosion comprises superficial rasping by various grazers as well as internal destruction by borers. The aim of this study is to present quantitative data on the boring of coral reefs by macro-organisms (macroboring) for the period mentioned. The rasping action of echinoids, fishes and molluscs so important in modern reefs has not been considered here for two reasons: firstly, the preservation potential of grazing traces is very low (Bromley and Asgaard 1993); and secondly, the organisms responsible for this type of bioerosion in modern reefs had not yet evolved. Microborers, such as Cyanobacteria, Chlorophyta, Rhodophyta and fungi have neither quantitatively nor qualitatively undergone large changes during the last 300 millions of years (Vogel et al. 1995) and may hence be equally excluded from this study.

Materials and Methods

Among the trace fossils produced by macroborers, the relationship to their producers is known in most cases (e.g. Bromley 1994) because borings broadly match their producers’ body outline. Identification of macroborings in fossil corals thus gives a fair clue to the bioeroders responsible for them. The observed diversity of borings need not fully mirror the original borer association, however, as there is no one-to-one relationship at least at the genus level. On the other hand, this restriction remains the same throughout the fossil record and hence does not distort the results of studies on bioerosion, as long as only the traces are considered.

Macroborings may be preserved differently at different localities; this may affect the methodology of their recognition. In the cases studied here, however, preservation of borings is rather uniform. Vertical sections through coralla or weathered surfaces allowed simple counting of borings crossing the relevant surfaces. The countings were then standardized to the surfaces measured and are subsequently given as the abundance of borings per square centimeter (Table 1).

Most borings observed are rather small (diameter below 1 cm) but some larger bivalves had already been active. Sponges, especially the family Clionidae, may be made responsible for the ichnogenera Entobia, Dendroreta and Dendrina, which have been recognized in the samples. Polychaete worms made macroborings of the types Caulostrepsis and Macandropolydorya; Trypanites could have been produced by this group as well as by Sipunculida. Bivalve borers of the families Mytilidae and Gastrochaenidae are deduced from their ichnotaxon Gastrochaenolites, and acrothoracic Cirripedia typically produce the trace fossil Rogerella. Based on the identification of these ichnogenera, the absolute and relative importance of the relevant borer group was inferred.

The sampling was designed as to include localities from various ages across the Triassic/Jurassic boundary. Within each stratigraphical stage, localities represent different environments (according to previous authors), especially with either turbid or clear conditions:

- Reiter-Alpe, northern Tyrol, Austria: Wettersteinkalk, Late Ladinian, Middle Triassic. This unit has to be attributed to a clear-water upper-slope or fore-reef environment remote from the coast; dendroid and solitary

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corals grew in low bioherms with various algae below the storm-wave base (Henrich 1983).

- **Hoher Göll, Salzburg Alps, Austria**: Dachsteinkalk, Norian, Late Triassic. The area comprises a complex mixture of facies types. Reefs constructed by sponges, algae and corals all grew in shallow, turbid, clear water (Zankl 1969).

- **Naybandan, northern Iran**: Nayband Fm, Norian, Late Triassic. Corals occurred in patch reefs here (pers. comm. B. Senowbari-Daryan) and exhibit a highly variable degree of bioerosion. Repeated influx of clay-to silt-sized siliciclastics was common judging by ragged outlines of massive coralla. The fill of the borings is mainly silt as well but this may have occurred after the conditions of reef growth or borer attack had changed.

- **Feichtenstein reef 12 km east of Hallein, Salzburg; Austria**: Rhaetian, Late Triassic. Starting from isolated patches, this well-zoned reef grew rather distant from the shore above the stormwave base (Schäfer and Senowbari-Daryan 1981) on a shoal rising from muddy surrounding.

- **Adnet reef 3 km east of Hallein, Salzburg, Austria**: Late Rhaetian, Late Triassic. Patch reefs at this locality were subjected to occasional siliciclastic influx in various environments through time, from protected lagoon to open shelf (Schäfer and Senowbari-Daryan 1981, Bernecker et al. 1999).

- **Moulay Idriss, High Atlas, Morocco**: Early Pliensbachian (Carixian), Early Jurassic. Coarse clastic material from adjacent land areas was shed into the surrounding shallow seas with numerous small patch reefs (Dresnay 1971, Beauvais 1986).

- **Beni Tadjit, High Atlas, Morocco**: Late Pliensbachian (Domerian), Early Jurassic. Groups of patch reefs developed in agitated water on a shallow carbonate platform with occasional sedimentation of coarse bioclastics (Dresnay 1971, Beauvais 1986).

### History of Triassic / Early Jurassic Coral Reefs

Understanding the history of macroboring requires some knowledge of the changes in its substrate, i.e. the reefs. During the Ladinian, corals mainly inhabited deep-water mounds; high-energy reef tracts were dominated by red algae and calcareous sponges. In the Carnian, they established themselves in reef-crest environments (e.g. Fürsich and Wendt 1977). The diversity of scleractinians rose throughout the Middle and Late Triassic, paralleled by an increasing percentage of cerioid forms against equal importance of solitary and dendroid taxa through time (Fig. 1, Riedel 1991). This was probably related to the acquisition of zooxanthellae as symbionts in the Carnian or Norian (Stanley 1988, Stanley and Swart 1995), facilitating a closer integration of the polyps. From the Norian onwards, scleractinians are found in reefs as builders (Flügel and Stanley 1984, Stanley 1988).

During the Late Rhaetian, corals were reduced from 67 to 18 genera globally (Riedel 1991), which lead to a phase without any reefs at all during the Hettangian. The lost ecosystem slowly recovered. The first Jurassic reefs are known from the Sinemurian and were built by various organisms including dendroid corals in different settings (e.g. Stanley and McRoberts 1993). During the Pliensbachian, scleractinian reefs had already established large reef tracts in Morocco (Dresnay 1971) and northeast Asia. Corals had become the dominant reef-builders again by the Bajocian (Middle Jurassic; e.g. Stanley 1988).

### History of Coral Diversity (Genera) during the Triassic

![Fig. 1 Distribution of scleractinian growth forms in the Triassic (data from Riedel 1991).](image-url)
Table 1 Percentage values of bioeroder groups (sponges to cirripeds) and overall abundance (as borings/cm²) at the study sites

<table>
<thead>
<tr>
<th>AGE</th>
<th>LOCALITY</th>
<th>AVERAGE PERCENTAGES</th>
<th>overall abundance</th>
<th>area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>sponges  bivalves  worms  cirripeds</td>
<td>(borings/cm²)</td>
<td></td>
</tr>
<tr>
<td>Ladinian</td>
<td>Reiter-Alpe, Austria</td>
<td>0       2600                0.01     2600</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Norian</td>
<td>Hoher Göll, Austria</td>
<td>0       0                   0.01     1660</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Norian</td>
<td>Naybandan, Iran</td>
<td>27.3     57            15.6     0.14  8786</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhaetian</td>
<td>Adnet, Austria</td>
<td>11.1     25.2         60.3     3.3    0.09  3556</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhaetian</td>
<td>Feichtenstein, Austria</td>
<td>40.3    59.6            0.11     1048</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carixian</td>
<td>Moulay Idriss, Morocco</td>
<td>2.5     46.2         31.1     20.2    0.12  977</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Domerian</td>
<td>Beni Tadjit, Morocco</td>
<td>3.3     11            50.6     35.2    0.08  1062</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Results

The results of the detailed evaluation of the samples described above (Table 1) may be generalised as follows: only microborings were found in the Ladinian Wettersteinkalk. In the clear-water Norian reef system in Salzburg, bioerosion was performed by very few bivalves and sponges; their abundance, however, was below 0.01/cm². The penecontemporaneous but turbid-water Naybandan reefs, on the other hand, saw “worms” dominating over bivalves and cirripeds (overall abundance 0.14/cm²). This situation persisted into the Rhaetian, when “worms” at Adnet (Austria) were more important than bivalves, sponges, or cirripeds; overall macrobioerosion also remained slight (0.09/cm²). The isochronous reefs in clear water lacked sponges and cirripeds but bioerosion remained little intense (0.11/cm²). As a caveat, these numbers refer to countings in vertical sections (first two examples and Rhaetian) and on the surface (Naybandan) and hence may perhaps be not fully comparable.

After the extinction, i.e. in the Pliensbachian, “worms” continued to outcompete bivalves in bioerosion, and cirripeds were important again; very few sponges were present. The intensity of boring continued at low levels independent of the facies (0.08 and 0.12/cm², respectively).

Fig. 2 Quantitative and qualitative distribution of borings in turbid shallow-water habitats; long vertical bars indicate system boundaries, short vertical bars indicate stage boundaries.
Fig. 3 Quantitative and qualitative distribution of borings in clear shallow-water settings; long vertical bars indicate system boundaries, short vertical bars indicate stage boundaries.

Summarising, bioerosion was sparse throughout the time span investigated; various “worms” were important borers continuously. The end-Triassic extinction of corals did affect their borers independently of the environment; this happened qualitatively but not quantitatively. The post-event reefs of the Pliensbachian saw a comeback of cirripeds as borers, again independently of the environment. This group had largely been ousted from reefs by the Rhaetian before. Triassic bioerosion was remarkable in turbid waters first (in the Norian, Fig. 2); reefs in clear water settings did not become attacked before the Rhaetian (Fig. 3). Also, sponges occurred as borers in turbid settings first (and their beginning success might have been suffocated by the end-Triassic scleractinian extinction). Clear-water bioerosion, in contrast, went almost without sponges throughout the time interval investigated here.

Discussion

The results of this study corroborate the pilot publication by Perry and Bertling (2000). Furthermore, they fit the sporadic mentioning of macroboring which was given in previous literature rather well. Judging these results, however, it has to be kept in mind that very few localities and only a limited number of corals were available at the time being. The environment of each single coral during its bioerosion is almost impossible to state with absolute certainty from the rock record. A caveat hence has to be put to generalisations.

Early Middle Triassic (Anisian and Ladinian) reefs built by corals or bivalves were very sparsely bored by cirripeds (Senowbari-Daryan et al. 1993) or phoronids (Hagdorn 1997). The information available for Carnian reefs (Fürsich and Wendt 1977) with their exclusively cirriped boring suggests persistence of this situation. The earliest Mesozoic boring bivalves have been reported from Norian deep- and turbid-water patch reefs (Frech 1890) as indicated by this study as well. Cirripedia were important still in the Norian but the pattern seems to have been heterogeneous. In the Alpine upper Rhaetian, no macroboring was detected in the deep fore-reef by Kuss (1983); it is reported to have been most intense in shelf-edge reefs (Roniewicz 1974, Michalik 1982). The moderate values of bioerosion, with bivalves and "worms" dominating independent of shallow nearshore environments, was modified by the first (localised but) remarkable contribution of sponges whereas cirripeds had lost their importance.

The earliest Jurassic (Sinemurian) reefs built by bivalves continued the pre-extinction bioerosion pattern with bivalves, sponges and "worms" as borers (pers. obs.). The first Liassic coral reefs were equally sparsely eroded (Stanley and Beauvais 1994) but the borer biology is not known. Pliensbachian reefs in Morocco remarkably exhibit a bioerosional pattern somewhat similar to the Triassic situation. During the latest Liassic (Toarcian) and early Dogger (Aalenian), bivalves came to dominance above all other borers and continued to do so throughout most of the Jurassic (Perry and Bertling 2000).

Trying to compare these results with patterns across other crises in reef history proves difficult because of the scarcity of data. No other studies apart from the few evaluated by Perry and Bertling (2000) are currently available. The same essentially applies to continuous studies of the biota of other hard substrates (e.g. rockgrounds and hardgrounds) in the time slice studied here.
Conclusions

The pattern of coral bioerosion remained similar regarding importance and overall style throughout the Late Triassic/Early Jurassic reef crisis. Quantitatively, abundance values stayed within a range of 0.08 to 0.12 borings per square centimetre. Qualitatively, various worm groups were the most prominent borers, with bivalves coming second; cirripeds were much more important than during other times of reef history (cf. Perry and Bertling 2000).

There seem to have been significant effects of the environment during phases of innovation in the boring association: In the Norian, noticeable macroboring originated in turbid nearshore settings when corals for the first time built shallow-water reefs. With the formation and extension of coral reef tracts, their borers spread seaward in the Rhaetian. Boring sponges initially were restricted to coastal environments rich in fine siliciclastics (and hence, presumably, nutrients). Apart from these short intervals, growth conditions of early Mesozoic reefs obviously did not control the qualitative or quantitative composition of its destroyer association to a large extent.

Rather than being governed environmentally, Late Triassic/Early Jurassic borers exhibit effects of parallel evolution with their scleractinian hosts. Major innovations in macroboring (boring bivalves in the Norian, boring sponges in the Rhaetian) occurred early during peaks of reef development. The end-Rhaetian extinction of reefs deprived boring sponges of their habitat and precluded their rapid re-establishment during the Liassic. At this time, the “clock was set back” and cirripeds re-entered coral reefs in all environments. (It is interesting to note that solitary borers obviously had an advantage over the colonially organised sponges). Progressive changes in the pattern of macro-bioerosion were hence linked to flourishing phases of reefs, although the long crisis affected the borers qualitatively.

There is no indication that borers contributed to the end-Triassic reef decline. In this case, increasing values of bioerosion should have been noticed, and the abundance of borings should have been much higher. The Mesozoic origin of boring sponges in the Rhaetian likewise was not responsible for the succeeding reef decline because sponges were not found in offshore settings. In any case, borers only reacted to substrate changes and did not bring them about.

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References


