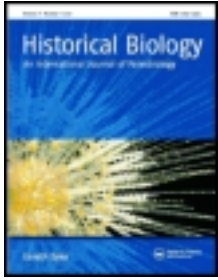


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Ecological signature of the end-Triassic biotic crisis: what do bivalves have to say?

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In order to understand the causes underlying the Triassic–Jurassic (T/J) mass extinction, we tested different bivalve features for extinction selectivity, i.e. shell mineralogy, age at the Rhaetian and three main autoecologic traits (feeding mechanism, tiering and motility/attachment). Also, diversity and turnover rates throughout the Triassic and the Early Jurassic were analysed in detail. The dataset employed for this analysis was a precise database at genus level including data from Induan to Sinemurian times. Results point to a true mass extinction for bivalves around the T/J boundary. This extinction was not age-selective at the boundary. Certain analyses suggested that shell mineralogy was a character significantly increasing survival odds, but this relationship seems to reflect selectivity on autoecologic traits. There was no difference in extinction proportions between both feeding types (i.e. deposit feeders and filter feeders); among the other traits, deep burrowers, epifaunal-motile and endobysate forms seem to have been favoured, while shallow burrowers (and probably reclined forms) were more heavily affected. This pattern suggests an environmental stress at the boundary with some particular issues affecting the different life modes. Models linking magmatism in the Central Atlantic Magmatic Province with the end-Triassic mass extinction are a plausible scenario for this kind of perturbation.

Keywords: end-Triassic extinction; Bivalvia; selectivity; shell-mineralogy; autoecology; CAMP

Introduction

Scientific interest on mass extinctions has grown exponentially over the last few decades since Raup and Sepkoski (1982) identified the commonly known ‘big five’. This interest was focused mostly on the Permian–Triassic (P/T) and Cretaceous–Tertiary (K/T) extinctions, and to a less degree on the other three events (Twitchett 2006). Of these, the Triassic–Jurassic (T/J) boundary mass extinction is probably the most controversial due to facies changes and the worldwide scarcity of complete and fossil-bearing sections (Hallam and Wignall 2000; Hallam 2002), although it was extensively studied in the last decade. It was even argued that this event should not be regarded as a ‘mass extinction’ since (a) it seems to have been more related to low origination rates combined with moderately high extinction rates, rather than merely to high peaks of extinction rates as happened around the P/T and the K/T (Bambach et al. 2004; Bambach 2006; but see Alroy 2008); nevertheless, if the criterion to define a mass extinction is the drop in diversity (see Bambach 2006 for a discussion on the concept of mass extinction), the T/J must be considered as one of the ‘big five’ and (b) the magnitude attributed to this event may be an artefact due to the ‘compiled correlation effect’ acting on a large amount of stratigraphically imprecise data, the ‘Signor–

Lipps effect’ (Signor and Lipps 1982), and the extrapolation of local evidence to global levels (Tanner et al. 2004; Lucas and Tanner 2008). These authors argued that the end-Triassic extinction was not just a catastrophic event at the end of the Rhaetian, but a combination of high extinction rates and low origination rates during the whole of the Late Triassic instead.

Marine bivalves are examined here as a detailed study case to evaluate the selectivity of the extinction in relation to different traits linked to the extinction odds of a taxon. Many authors dealt with the issue of selectivity during mass extinctions in order to correctly understand their causes (Kitchell et al. 1986; McRoberts et al. 1995; McKinney 1997a; Aberhan and Baumiller 2003; Jablonski 2005, 2008; Kiessling and Aberhan 2007a; Janevski and Baumiller 2009). The following traits (among others) were studied: feeding type (Rhodes and Thayer 1991; Jablonski and Raup 1995; Kiessling et al. 2007), tiering (McRoberts and Newton 1995; Kiessling et al. 2007), size (Hallam 2002; Rivadeneira and Marquet 2007), geographic range (Jablonski and Raup 1995; Rivadeneira and Marquet 2007; Finnegan et al. 2008), age (referring to the duration of the taxon in the geologic record, either counted in million years or in time bins – e.g. stages) at the moment of extinction (Van Valen 1973; Finnegan et al. 2008), shell

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mineralogy (Hautmann 2006; Kiessling et al. 2007), substrate preferences (Kiessling et al. 2007; Peters 2008), motility (Kiessling et al. 2007), specific richness (Finnegan et al. 2008) and abundance (McKinney 1997b; Simpson and Harnik 2009).

In this paper, attention is focused on some of these traits, particularly the ecologic ones (feeding type, tiering and motility/attachment), but also shell mineralogy and genus age at the end of the Rhaetian. Since the database here used is a new worldwide compilation of genus-range taxa at the stage level for marine bivalves applying a uniform taxonomic concept and a single stratigraphic scheme, we re-examine the previous conclusions on these topics, and try to provide new evidence to some discussions on the matter. Ros and Echevarría (2011) used this same database to discuss aspects of systematic and ecological diversity dynamics which complement this study.

Database and methods

Database

Our primary data source is Ros (2009), freely available online and downloadable from <http://tdx.cat/handle/10803/9952>, with a revision of the stratigraphic ranges of megalodontids based on Végh Neubrandt (1982). This database provides data on stratigraphic range, paleogeographic distribution, autoecology and shell mineralogy of all marine bivalve genera in the time interval ranging from Induan (Early Triassic) to Sinemurian (Early Jurassic; summarised data in Ros 2009, pp. 366–374). It is a critically updated compendium where data of every genus and its constituent species were carefully revised, and only records accompanied by full descriptions and figures were included. The species were considered to check the diverse systematic interpretations by different authors. For example, the species *decidens* Bittner, 1899, was proposed within the genus *Pseudomonotis*; later some authors assigned it to *Streblochondria* and *Claraia* and subsequently it was assigned by Newell and Boyd (1995) to *Crittendenia* and as the type species of *Claraia* (*Bittnericlaraia*) by Gavrilova (1996). If species were not considered, we would have three spurious records.

In order to minimise taxonomic and stratigraphic inconsistencies, advice was sought – whenever necessary – from the experts on different subgroups or specific geographic areas. Although no data were downloaded from the Paleobiological Database (PBDB; Alroy et al. 2001; <http://www.paleodb.org/>), this database, as well as Sepkoski's (2002) compendium, was consulted as reference for some data and to localise bibliography.

The unit used in this database is the genus because it is regarded as the lowest taxonomic category stable enough to perform this kind of macroevolutionary analysis.

Although the use of subgenera is frequent in the literature (Raup 1978; Jablonski et al. 2003), the experience shows that in several cases subgenera were erected taking into account specific level criteria; sometimes even superficial shell structures easily influenced by taphonomic processes were used to diagnose subgeneric taxa. The families Entoliidae or Halobiidae provide good examples [Ros 2009; see also Johnson (1984) and Damborenea (2002) for the family Entoliidae and McRoberts (1993, 2000) and Campbell (1994) for the family Halobiidae]. The use of subgenera in order to minimise the 'Pull of the Recent' (Raup 1972, 1978) is not pertinent in this case, since no stratigraphic range was extended in the analysed time interval due to the presence of an extant species. The genus *Acharax*, recorded before and after the study interval but not during it, which is also very similar to the genus *Solemya*, was excluded from the analysis.

We follow the systematic arrangement by Amler (1999) and Amler et al. (2000) with some modifications discussed in Ros (2009). The stratigraphic resolution of our analyses is stages with the values for their boundaries taken from Gradstein and Ogg (2004). Different time scales in the analysed papers were updated using the conversion tables in PBDB and GeoWhen (<http://www.stratigraphy.org/geowhen/index.html>). Although, the Triassic time scale is still unstable (Schultz 2005) since most boundary stages lack a definite Global Standard Section and Point, Ros' (2009) database was based on a well-defined stratigraphic scheme linked to absolute ages. When this scheme could not be directly applied (either because the papers were too old, the authors did not follow it, or the stratigraphic assignment of the records was too vague), the stratigraphic provenance was carefully checked and adjusted to this scheme. Even if the interpretation of the stages may change in the future, the database will still be as robust as those absolute ages. A special problem was the stratigraphic provenance of Norian and Rhaetian faunas in papers published between Tozer (1979), who initiated the tendency of relegate the Rhaetian as Norian substage, and the redefinition of Rhaetian by Dagys and Dagys (1994; see discussion in Hallam 2002). At least the Kössen Formation in Austria, the Gabbs Formation in USA and the Otapirian deposits in New Zealand were considered to be truly Rhaetian in age (Dagys and Dagys 1994; Hallam 2002; Cooper 2004). The age of other units from the Norian–Rhaetian interval were carefully verified, so the resolution for these data is significantly improved over previous databases. Time ranges used here are observed ranges, defined by first appearances (FADs) and last appearances (LADs), and therefore they are only proxies for actual origination and extinction times. It must be taken into account that sample biases, stratigraphic gaps, transgression and regression effects, and many other factors, can affect first and last appearances (Holland

1995). Also, those bivalve temporal ranges are especially influenced by lithologic facies.

Selectivity traits categorisation

In order to test for selectivity at the end-Triassic mass extinction, we considered the traits explained below. Many of these traits, together with taxonomic diversity, were analysed along the Induan–Sinemurian interval (Ros and Echevarría 2011) and, since this paper is a complement for that analysis, categorisation was maintained for consistency.

Autoecological traits

Different aspects related to life habits were subjected to selectivity studies among bivalves at the T/J extinction. Kiessling et al. (2007) found no difference between the two main feeding types (deposit and filter). Regarding tiering, many papers document preferential extinction of infaunal bivalves over epifaunal ones, either at a regional scale (in European faunas: McRoberts and Newton 1995; McRoberts et al. 1995; in British Columbia: Wignall et al. 2007; Wignall and Bond 2008; in Tibet: Hautmann et al. 2008b) or at a global scale (Kiessling et al. 2007). On the other hand, other results show no such preference, but instead they argue for differences in the extinction rates before the Rhaetian, when epifaunal bivalves suffered higher levels of extinction (McRoberts 2001). We analysed three main factors: feeding type, tiering and degree of motility/attachment, the same considered by Bambach et al. (2007) for the establishment of the animal marine ecospace. The assignment of taxa to either of these broad ecological subdivisions was based on autoecological literature, analysis of functional morphology and/or analogy with living relatives of similar morphology. See discussion of mode of life of each genus in Ros (2009). The feeding type includes only two categories: filter feeders versus deposit feeders, as carnivorous bivalves (e.g. Septibranchia) did not appear until the Middle Jurassic. Because deposit feeders are all shallow burrowers, the feeding type was analysed separately from other traits and only in that ecological group. Three other categories were defined for the tiering: epifaunal, shallow infaunal and deep infaunal. Endobysate, semi-infaunal bivalves were grouped with the infauna, as they burrow to a certain degree and so share some of the physical needs and limitations of this category. On the other hand, free lying bivalves whose semi-infaunal habits rely on their heavy massive shell instead of active burrowing (e.g. some megalodontids) were grouped with the epifauna. Other three categories for the degree of motility/attachment were established: attached, sedentary and motile. Tiering and motility/attachment were analysed as interacting factors, with intersection of the categories of

both traits resulting in a reduced ecospace of nine categories, of which only six modes of life were occupied by bivalves in our study interval: epifaunal-attached (either epibyssate or cemented), epifaunal-sedentary (reclined, including the semi-infaunal ones), epifaunal-motile (swimmers, facultative swimmers and pseudo-planktonic), shallow infaunal-motile (shallow burrowers, either filter feeders or deposit feeders), shallow infaunal-attached (endobysate), and deep infaunal-sedentary (deep burrowers). Those attached genera having the ability to detach and move temporally were included in the motile category, since we assumed that higher motility would be an advantage under environmental stress (although it can also be a disadvantage since higher motility requires more energy). All genera that during their adult life do not attach (either by a byssus or by cementation) and practically do not move (although they can have high motility as juvenile or can become attached during settlement) were considered as sedentary; the genus *Solemya*, although motile as adult, was grouped with the remainder deep-burrowers, which are sedentary. The boring genus *Lithophaga* was coded as shallow infaunal attached. The genus *Pichleria* was considered as infaunal, but could not be codified for a motility/attachment category. Many of these categories are amenable to be subdivided in more precise subcategories (Ros et al., 2011), but since we are looking for broad trends we had to consider certain generalisations. Nevertheless, the main groupings within each category were also compared in the corresponding sections.

For comparison between infaunal and epifaunal bivalves, both categories for infaunal habit were grouped together. For these broad categories, turnover rates were also calculated.

Shell mineralogy

Shell mineralogy was also suggested as an aspect associated with the survival chances of bivalves during the T/J extinction. Hautmann (2004, 2006) and Hautmann et al. (2008a, 2008b) suggested that epifaunal bivalves with thick aragonitic shells were more affected by the extinction, a fact they related to a change in the sea chemistry (Sandberg 1983) from aragonitic-favourable to calcitic-favourable sea conditions during the T/J transition (but see also Kiessling et al. 2007, p. 219; Mander et al. 2008). We included this trait in the analysis by taking into account two categories: aragonitic (all shell layers are aragonitic) and biminerale (at least one of the shell layers is calcitic). Data were compiled from Taylor et al. (1969, 1973), Carter (1990) and additional publications cited in Ros (2009). As shell mineralogy is strongly correlated with the life habit, as all infaunal bivalves are aragonitic, a particular analysis was also performed on the epifaunal bivalves only, as proposed by many authors (Hautmann

2006; Kiessling et al. 2007; Hautmann et al. 2008a, 2008b).

Genus age at the Rhaetian

Van Valen (1973) concluded that extinction risk was independent from the age of taxa, but during the following years many authors demonstrated that longevity can indeed influence extinction risk (Raup 1975; Gilinsky 1988; Boyajian 1991; Finnegan et al. 2008). In our analysis, we considered age of genera in millions of years, instead of number of stages due to the high variability in the duration of the different stages included in the interval (from 1.3 million years for the Induan to 12.9 million years for the Norian). As a consequence, the age of the genera at the extinction event is a continuous variable. Perhaps considering the mid-point of the stages of FAD and LAD might produce a more accurate value, but this would imply a different criterion for the singletons (otherwise they should be coded as zero-agers). To avoid this, we prefer to consider the base of the FAD stage as the earliest appearance for the genus and the top of the LAD as its last appearance, although the ages of the genera may thus result somewhat overestimated.

Although geographic range was usually considered as a factor potentially related to survival during extinction events (Hallam 1981; Jablonski 1986; Jablonski and Raup 1995; Kiessling and Aberhan 2007b; Rivadeneira and Marquet 2007), we have not evaluated that trait in this paper, leaving it for further study.

Methods

Assessment of diversity dynamics

In order to analyse the changes in diversity we used the Boundary Crossers metric (i.e. for a stage boundary we counted the taxa present before and after the boundary; Sepkoski 1979; Alroy 1996; Foote 2000) as estimator, since it is a precise measure of the taxa present at a time point. To standardise the origination and extinction rates, mean standing diversity (MSD) was calculated by summing all the continuous ranges, one half for each LAD and FAD (Foote 2000) and one-third for each singleton as justified by Hammer (2003, p. 306) and Hammer and Harper (2006). Origination rate was calculated as the number of FADs divided by MSD and standardised by the length of the stage, while extinction rate was obtained as LADs divided by MSD and also standardised by the length of the stage; diversification rates were calculated by the subtraction of extinction rate from origination rate (Sepkoski 1978). Although standardising by stage length has been questioned (see Foote 2005), we must consider the differences in length between stages during the Triassic (up to an order of magnitude);

also there are some suggestions of high extinction rates along the whole Late Triassic instead of pulsed extinction. Thus, we considered standardisation by stage length as a more parsimonious (and probably less biased) approach. In the analysis of extinction selectivity, singletons and first originations were always included. When interested only in diversity changes through time, then it would be useful to avoid singletons and work only with boundary-crosser data, as explained by Bambach et al. (2004), but in order to understand the diversity dynamics within each stage we needed to consider singletons too. If singletons were excluded, then evolutionary rates would be underestimated and would not reflect the true diversity dynamics of different stages (e.g. one stage can have the same number of taxa at the beginning and at the end, but the dynamic within the stage will be different if we have high instead of null turnover rates). These same diversity estimators were used by Ros and Echevarría (2011) once again for maintaining a unique criterion.

Extinction selectivity

For the analysis of extinction selectivity, two main strategies were applied. On one hand, the observed proportions of extinct genera were compared to the expected ones by assuming random extinction among categories. When the comparison was between only two categories, a chi-square test was applied, while for three or more categories a resampling algorithm, similar to that applied by Smith and Roy (2006), was used to check which categories (if any) depart from the expected values. Taking into account the number of genera belonging to each category, the number of surviving genera was drawn randomly among them (without replacement); after that, we checked in every category if the number of sampled genera was higher, equal or lower than the actual number of survivors. By repeating this procedure 10,000 times, we calculated the probability of obtaining the actual values (or higher or lower values) by chance. Since what we wanted to know was if the real values were significantly different from the values produced randomly, the proportion of iterations that were equal to the observed values were added to the other two categories; consequently the resulting tables show the probability of obtaining by chance equal or lower values than those observed, and the probability of obtaining by chance equal or higher values than those observed. For this analysis, an R code was developed (R Development Core Team 2008). In order to test for the reliability of the code, we repeated the analysis but sampling the extinct instead of the survivor genera, obtaining similar values. In this case the null hypothesis is that the extinction proportion on each category is not distinguishable from random extinction among categories, and the significance level was $p < 0.025$ since it is a two-tailed test (we were looking for significantly higher or

lower values than those expected by chance). The chi-square test was performed in PAST (Hammer et al. 2001), and in this case the significance level was $p < 0.05$ (we were looking for differences in two means).

On the other hand, a generalised linear model (GLM) was applied to both the continuous and the categorical features of the analysed genera. GLM is useful when the variance is not constant and/or when the errors are not normally distributed; binary response variables (in this paper, extinct – 0 – or survivor – 1) are a case where using GLM might be considered (Crawley 2007). For every trait analysed, we provide the linear predictor (in the ‘Estimate’ column on each table). Positive linear predictors imply higher chances of survival, while negative linear predictors represent higher chances of extinction. Significant values of p result in linear predictors considered as different from zero, implying that the considered trait has a significant influence in survival odds, either increasing them (if the linear predictor is positive) or reducing them (if the linear predictor is negative). The GLM was performed in R using the function ‘glm’ from the package ‘faraway’.

For GLM analysis with more than one trait, a model simplification was applied (Crawley 2007) in order to evaluate the significance of the explanatory variables. In this case, the way to estimate the best explanatory power of two models was the Akaike information criterion.

Although the significance level used was 0.05, we also remarked p -values between 0.05 and 0.10 as within the significance limit (or between 0.025 and 0.05 for the resampling algorithm). Due to the low number of observations, we consider these values as potentially explanatory variables, even though not truly significant.

Three main comparisons were done: one for the autoecological characters, one for the genus age and one for the shell mineralogy. This was necessary due to the large number of traits along with a relatively low number of observations (124 genera for the Rhaetian); the traits were grouped by taking into account the possible interactions between them (e.g. the autoecological characters will have stronger interactions between them than with the genus age). Nevertheless, for mineralogy, which seems to have a strong correlation with some autoecological traits, we performed an analysis including both traits in order to check for this possible interaction.

Results

Assessment of diversity and evolutionary rates

When analysing the evolutionary rates of the whole data set (Figure 1), the differences between the measured values for the Rhaetian and the Triassic means of extinction and origination rates are evident. The arrows show those differences (the horizontal dashed lines represent the mean values for the Triassic of both rates),

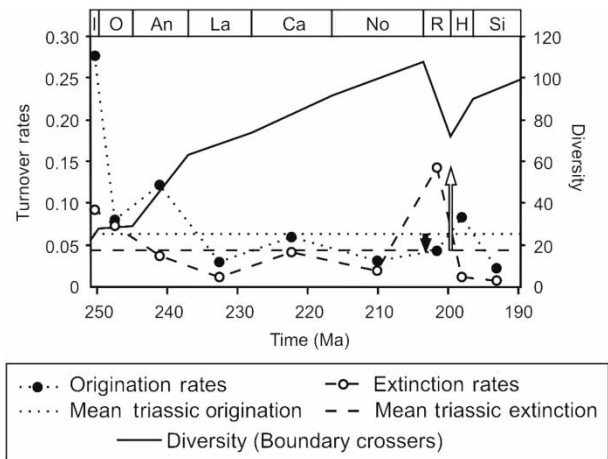


Figure 1. Diversity and evolutionary rates during the study interval: right scale, diversity in number of Genera (Boundary Crosser estimation); left scale, evolutionary rates in $\text{genera} \times \text{genus}^{-1} \times \text{Myr}^{-1}$; solid line, measured diversity (boundary crossers metric); dashed line + empty circles, extinction rates; dotted line + filled circles, origination rates; horizontal dashed line, mean Triassic extinction; horizontal dotted line, mean Triassic origination; arrows showing differences in mean Triassic origination (black arrow) and extinction (white arrow) rates with the respective measured values for the Rhaetian. Abbreviations for stages: I, Induan; O, Olenekian; An, Anisian; La, Ladinian; Ca, Carnian; No, Norian; R, Rhaetian; H, Hettangian; Si, Sinemurian; modified from Ros and Echevarría 2011.

pointing to a clear peak in extinction intensity at that stage, while origination is quite close to the mean.

Concerning the evolutionary rates for infaunal and epifaunal bivalves (Figure 2), the extinction value during the Rhaetian is the same for both categories, but epifaunal bivalves tend to show higher extinction values in previous stages (Figure 2(A)). Nevertheless, this is compensated by higher origination rates for epifaunal bivalves (Figure 2(B)), and consequently diversification rates are very similar (Figure 2(C)), with main exceptions in the Carnian and the Hettangian.

Another analysis of diversity dynamics was carried out within epifaunal bivalves, this time discriminating by life habit (degree of motility/attachment) and mineralogy (Figure 3); here the contribution of the sedentary forms to the high extinction levels of the aragonitic bivalves is evident.

Selectivity of extinction

Autoecological traits

The chi-square analysis of the feeding type shows no significant difference in the extinction incidence between suspension feeders and deposit feeders ($p = 0.293$). The inclusion of the feeding type in the GLM performed on autoecological characters resulted in a non-significant

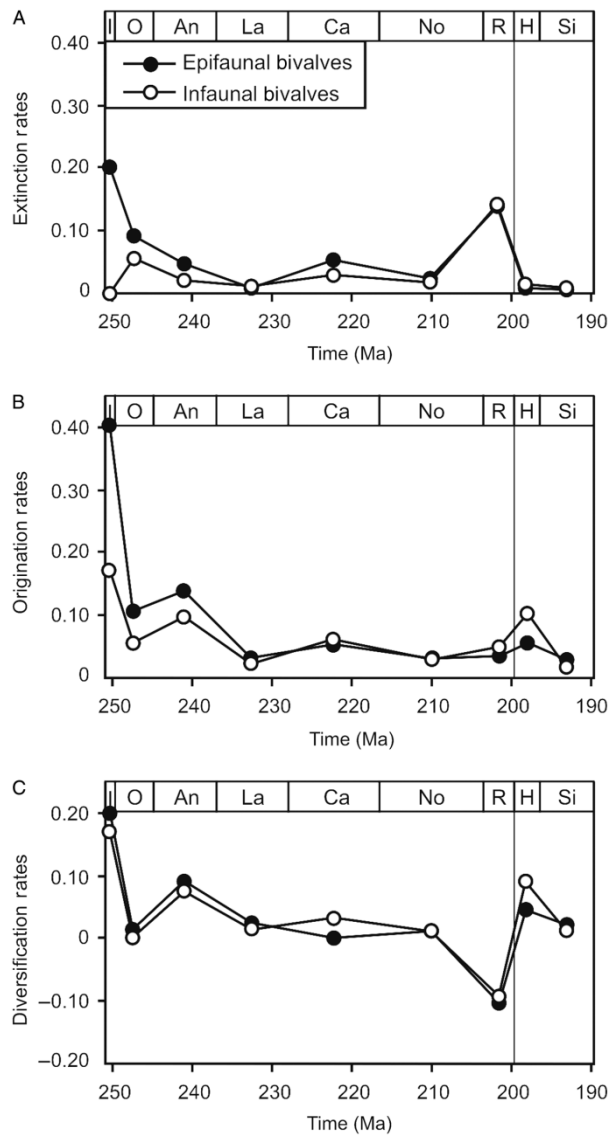


Figure 2. Evolutionary rates of epifaunal and infaunal bivalves – evolutionary rates in $\text{genera} \times \text{genus}^{-1} \times \text{Myr}^{-1}$. (A) Extinction rates; (B) origination rates and (C) diversification rates. Abbreviations for stages are mentioned in the caption of Figure 1.

value (i.e. this trait has no significant effect on the survival odds), and this trait was excluded by the stepwise model simplification. The chi-square test for extinction proportions between infaunal and epifaunal bivalves shows no significant differences ($p = 0.943$).

The resampling analysis of the interaction of the other two autoecological traits (Table 1) shows no significant results, with the exception of the shallow infaunal-motile category, which seems to have lower survivorship than expected by chance. Both the deep infaunal-sedentary and shallow infaunal-attached categories have low p -values, but they are not even at the limit of significance established

for the test (although this could be due to the scarcity of genera).

On the other hand, the GLM applied to tiering and motility/attachment shows a significant positive value of the linear predictor for the deep infaunal-sedentary and shallow infaunal-attached forms (Table 2), indicating that these habits were positively selected and confirming the trends shown by the resampling method. The linear predictor value (Table 2, 'Estimate' column) for the epifaunal-motile category should be considered at the limit of significance; although this category contained two groups that were different in their motility (i.e. pseudoplanktonic vs. swimmer), there is no significant difference between them in the proportion of extinction ($p = 0.793$ for a chi-square analysis).

Epifaunal-sedentary and epifaunal-attached categories show no significant values in any of the tests. For the epifaunal-attached (i.e. cemented and epibyssate) category, this is expected, since the extinction proportion ($14/34 = 0.412$) is very close to the general one ($50/122 = 0.410$); there is no significant difference between the two subcategories either ($p = 0.618$ for a chi-square analysis). But for the epifaunal-sedentary category, this seems to be a result of their low number, since they show the highest extinction ($6/9 = 0.667$) and lowest diversification rate of the autoecological categories (Table 3).

Shell mineralogy

For the GLM, the mineralogy seems to be highly significant when all genera are included in the analysis (Table 4A); nevertheless, since all infaunal genera are completely aragonitic, the analysis was carried out again by using only the epifaunal forms and the values are shown in Table 4C. It is evident that, although the p -value is not significant, it is low; similar results were obtained with the chi-square analysis ($p = 0.083$). Nevertheless, once the autoecological characters are included (i.e. motility/attachment), mineralogy is not significant any longer (Table 4B,D); Figure 3 shows this relationship between extinction and each mineralogy category by taking into account the epifaunal ecological categories. Figure 4 shows the diversity dynamics of both mineralogies (including all the ecological categories); if we compare it with that published by Ros and Echevarría (2011, fig 3A) for the ecological categories, we see how the curve for aragonitic shelled bivalves is very similar to the curve for shallow burrowers, while the curve for bimineralic-shelled bivalves is very similar to the curve for epifaunal attached forms. It must also be noted that the stepwise model simplification applied on the results for epifaunal forms (Table 4D) eliminated the mineralogy of the shell as a variable when looking for the best model.

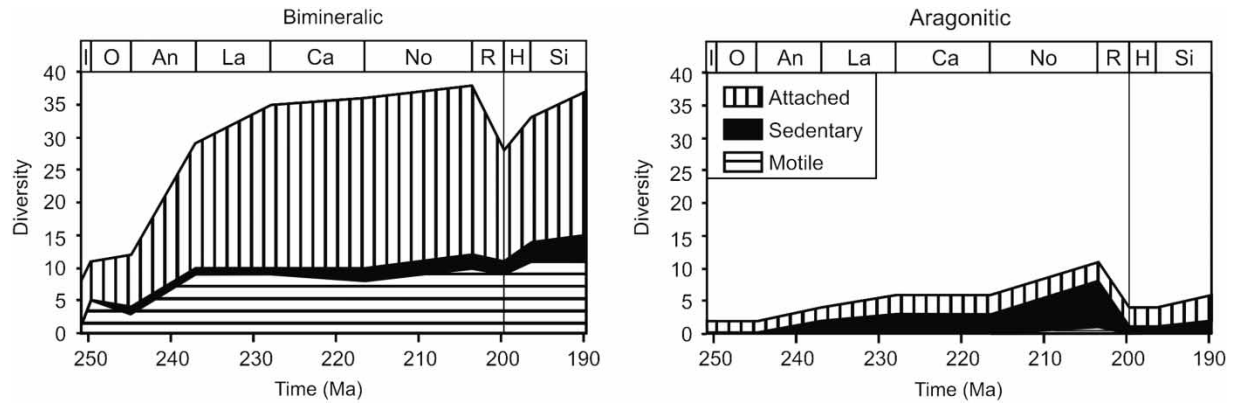


Figure 3. Diversity dynamics and shell mineralogy on epifaunal bivalves during the Triassic and part of the Early Jurassic – diversity in number of genera (Boundary Crosser estimation). Abbreviations for stages are mentioned in the caption of Figure 1.

Genus age

GLM performed for this trait resulted in no significant value (Table 5). Even taking into account the other variables in the analysis, age remained as a non explanatory variable, and it was always eliminated by the stepwise model selection.

Discussion

T/J event as a true mass extinction

Bambach et al. (2004) and Bambach (2006) postulated that the end-Triassic mass extinction was the result of a modest extinction peak accompanied by a drop in origination rates (but see Alroy 2008). The results presented here do not support this idea, at least for bivalves. There are high origination rates by the Early Triassic and the Anisian, but since the Ladinian the rates fluctuate between 0.030 and 0.060 genera × genera⁻¹ × Myr⁻¹ (Figure 1). The value for the Rhaetian (0.044 genera × genera⁻¹ × Myr⁻¹) is within this range, and it is even a bit higher than the Norian value (0.030 genera × genera⁻¹ × Myr⁻¹). Extinction rate, on the other hand, is highest during the Rhaetian (0.143 genera × genera⁻¹ × Myr⁻¹); this points to a true

mass extinction by the end of the Triassic, already detected by Hallam (2002, table 2) for bivalves and other organisms. The difference between the extinction rate and the average is quite large, while for the origination rate is rather small (Figure 1). Also, at a wider taxonomic scale, a decrease in the origination rate along the Triassic should be expected, since this period witnessed the recovery from the highest Phanerozoic depletion of diversity (Krug and Jablonski 2011); origination rates should be the highest immediately after the P/T boundary (Alroy 2008) and then, as diversity rises, they should decrease gradually. This is exactly what we see for the Early and Middle Triassic bivalves.

Comparison of extinction among tiering categories

Another frequently mentioned feature related to bivalve T/J extinction in regional studies is that it affected infaunal bivalves more than epifaunal bivalves (McRoberts and Newton 1995; McRoberts et al. 1995; Wignall et al. 2007; Hautmann et al. 2008b; Wignall and Bond 2008). Our results do not show this pattern, but instead we agree with the information provided by McRoberts (2001) and

Table 1. Results of the resampling analysis of the autoecological traits (excluding feeding type).

		Epifaunal	Shallow infaunal	Deep infaunal
A	Attached	0.5665	0.9829	–
	Sedentary	0.0982	–	0.9946
	Motile	0.9782	0.0188*	–
B	Attached	0.5897	0.0649	–
	Sedentary	0.9770	–	0.0565
	Motile	0.0985	0.9936	–

Notes: A, proportion of iterations that resulted in the same or lower number of survivors by chance; B, proportion of iterations that resulted in the same or higher number of survivors by chance. *Significant values ($p < 0.025$).

Table 2. Results of the GLM analysis applied to the autoecological traits (excluding feeding type) and survival during the Rhaetian.

	Epifaunal	Shallow Infaunal	Deep infaunal	
Attached	0.3567	1.3863	–	Estimate
Sedentary	–0.6931	–	2.0794	
Motile	1.5041	–0.1823	–	
Attached	0.3060	0.0317*	–	p
Sedentary	0.3270	–	0.0499*	
Motile	0.0544**	0.5470	–	

Notes: *Significant values ($p < 0.05$); **Limit of significance ($0.05 < p < 0.10$).

Table 3. Diversification rates during the Rhaetian among ecological categories (in genera \times genus⁻¹ \times Myr⁻¹).

	Diversification rates
Deep infaunal-sedentary	0.000
Shallow infaunal-attached	-0.020
Epifaunal-motile	-0.050
Epifaunal-attached	-0.089
Shallow infaunal-motile	-0.149
Epifaunal-sedentary	-0.250

Kiessling et al. (2007) which shows that the extinction rate is the same for both groups in the Rhaetian, but with higher rates for epifaunal bivalves during the previous stages (Figure 2(A)). Nevertheless, it is remarkable that the origination rates are also usually higher for epifaunal bivalves (Figure 2(B)), thus resulting in slightly higher, although probably no significant, diversification rates for this group during the Early and Middle Triassic (Figure 2(C)). So both diversification curves can be considered as very similar, with the major difference being in the Carnian – a stage with high turnover – when infaunal forms experienced a higher diversification, surpassing epifaunal ones in diversity, and again for the Hettangian stage, implying that infaunal bivalves recovered faster from the T/J event.

McRoberts and Newton (1995) and McRoberts et al. (1995), based on the supposed preferential extinction of infaunal bivalves over epifaunal bivalves, suggested a reduction in primary productivity as the main cause for the T/J extinction event. This was based on the differential abilities for filtering food observed between these two

Table 4. Results of the GLM for mineralogy of the shell.

		Estimate	<i>p</i>
A	Bimineralic shell	0.8044	0.0058*
	Aragonitic shell	-2.52E - 14	1.000
B	Epifaunal-attached	-0.7640	0.3314
	Shallow infaunal-attached	0.5724	0.4769
	Epifaunal-motile	0.4249	0.6788
	Shallow infaunal-motile	-0.1398	0.6476
	Epifaunal-sedentary	-0.9984	0.1880
	Deep infaunal-sedentary	2.0794	0.0499
	Bimineralic shell	1.2299	0.1078
C	Bimineralic shell	0.55962	0.0742**
	Aragonitic shell	-0.55962	0.3719
D	Attached	-0.3386	0.706
	Motile	0.8246	0.458
	Sedentary	-0.8772	0.244
	Bimineralic	0.7644	0.399

Notes: A, all genera included; B, all genera included, analysed together with the autecological categories; C, only epifaunal genera included; D, only epifaunal genera included, analysed together with the motility/attachment. *Significant values ($p < 0.05$); **Limit of significance ($0.05 < p < 0.10$).

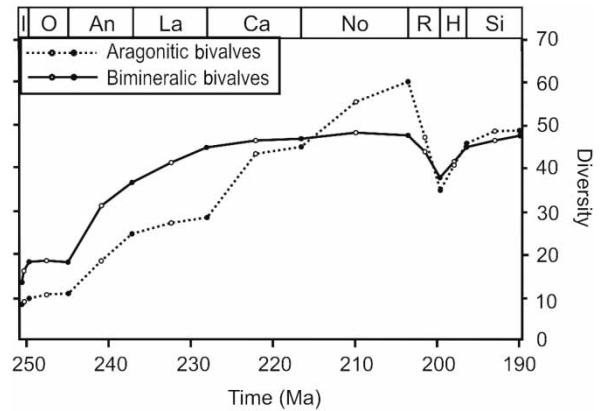


Figure 4. Diversity among the different shell mineralogy categories during the Induan–Sinemurian interval; filled symbols, diversity in number of genera (BC metric); empty symbols, diversity in number of genera (MSD metric). Abbreviations for stages are mentioned in the caption of Figure 1.

groups, since epifaunal bivalves usually have higher clearance rates than infaunal ones (Jørgensen 1975; McRoberts et al. 1995). Nevertheless, what we actually see is the same extinction rate for both groups during the Rhaetian, with slightly different diversity dynamics between them for other stages. Furthermore, a reduction in primary productivity would cause higher extinction rates among filter feeders than among deposit feeders (Rhodes and Thayer 1991), as this last group depends on the detritus chain, which would be less affected by such reduction [although Levinton (1996) argued against this idea]. Our data do not show such difference, and in fact extinction proportions between the two groups are statistically indistinguishable. Although a reduction in primary productivity cannot be discarded, our data do not support it as a main reason for the T/J extinction pattern among bivalves.

Survival selectivity on age of lineages at the Rhaetian

Although Van Valen (1973) – with his Red Queen hypothesis – proposed that extinction risk was independent of age, it was later demonstrated by many authors that age can indeed influence extinction risk (Raup 1975; Gilinsky 1988; Boyajian 1991). Finnegan et al. (2008), working with 11 Myr time bins, found that in most time bins greater ages produced higher survival odds, at least at genus level.

Table 5. Results of the GLM analysis applied to age of genera and survival during the Rhaetian.

	Estimate	<i>p</i>
Intercept	0.0901	0.7470
Age at the Rhaetian	0.0070	0.2850

Nevertheless, the terminal Triassic bin was one of the few where the non-selective extinction model could not be rejected. The data drawn from bivalves in our analysis support this.

Survival selectivity on shell mineralogy

In relation to shell mineralogy, Hautmann (2004, 2006) proposed that the higher extinction rates in aragonitic bivalves were due to a change in seawater chemistry produced by a decrease in the Mg^{2+}/Ca^{2+} ratio and the release of great amounts of CO_2 by volcanism. Such a change would cause an undersaturation of calcium carbonate minerals, resulting in a selective advantage for the secretion of the least soluble polymorph. The magmatic effusion produced by the Central Atlantic Magmatic Province (CAMP), which is dated around 196–202 million years ago, would certainly have released large amounts of CO_2 into the atmosphere (McHone 2003, Pálffy 2003; Schaller et al. 2011). The effect of the Mg^{2+}/Ca^{2+} ratio in this kind of shifts in seawater seems to be somewhat supported by experimental research. Checa et al. (2007) forced calcitic-shelled bivalves to secrete aragonite by changing the Mg^{2+} concentration [although the concentration they used was far higher than that expected for Mesozoic seas (Dickson 2002; Ries 2004)]. Effects of water acidification cannot be discarded either; Green et al. (2004) verified that waters undersaturated in aragonite increased mortality (and even dissolution in living forms) of small post-larval bivalves.

Nevertheless, this supposed extinction selectivity of aragonitic forms is not observed among all taxonomic groups. While some fully aragonitic taxa such as Scleractinia and sphinctozoid sponges were severely affected (Hautmann 2008b), others such as gastropods were barely affected by the extinction event, whereas calcitic brachiopods are strongly affected (Kiessling et al. 2007). Also, if size is a key issue in shell dissolution, it must be kept in mind that larval shells of all known bivalves are aragonitic, so they would be equally affected at this stage, no matter the mineralogy of adult forms. Although we found that shell mineralogy seems to increase survival odds among bivalves (Table 4A,B), this relationship disappears when autoecological traits are considered (Table 4C,D). Diversity dynamics among autoecological categories and among shell mineralogy categories show very similar patterns for shallow burrowers and aragonitic forms and for epifaunal attached bivalves and bimineralic forms, i.e. either the mineralogy is influencing the autoecological traits pattern or the autoecology is influencing the mineralogy pattern. Although selectivity for shell mineralogy in bivalves has a high statistical significance, we consider mode of life as a more biologically meaningful explanation of diversity patterns. Shell mineralogy is strongly correlated with

different life habits, probably rendering a better synthesis of survival odds than ecological categories themselves (i.e. shell mineralogy expresses a pattern similar to that for ecological traits with less parameters). All infaunal bivalves are aragonitic and, even among epifaunal forms, all the extinctions of aragonite-shelled bivalves except one are of forms with a reclined habit, which showed the lowest diversification rate (Figure 3 and Table 3). For this mode of life, five out of six extinct genera belong to the Megalodontoidea, which were all tropical forms probably dependent on photosymbionts for nutrition (Freitas et al. 1993; Yancey and Stanley 1999). Although not strictly reef organisms, they should be as vulnerable as reef communities, which were severely affected at the T/J boundary. Actually, tropical bivalve faunas were much more affected by the T/J extinction event than faunas from temperate and cold waters (Kiessling and Aberhan 2007a). Also, together with megalodontids, oysters were one of the bivalve lineages that showed no recovery during the first two stages of the Jurassic (Ros and Echevarría 2011), but they were ubiquitous in later faunas even building reefs. This clearly points to a calcification crisis (Hautmann 2004, 2006; Van de Schootbrugge et al. 2007; Hautmann et al. 2008a; Črne et al. 2011) but without selectivity for mineralogy. The absence – although one ghost lineage is inferred (Ros 2009) – of Hettangian megalodontid representatives, unlike oysters which were well represented but in low diversity, points to a well-known preservational bias: aragonitic shells have less chances than bimineralic shells of being preserved (Harper 1998; Bush and Bambach 2004; Ros and De Renzi 2005; Valentine et al. 2006; but see Kidwell 2005).

Survival selectivity among autoecological traits

Autoecological traits present a pattern of selectivity that appears difficult to explain. Selectivity for motility differs within the tiering categories: among infaunal forms, motility seems to be linked to higher extinction rates, while epifaunal forms show the opposite. Epifaunal-motile bivalves are expected to have higher survival rates than non-motile ones considering ecological disturbance. This is because they can move to avoid predators or to search for more suitable environments. At this point, we must consider the quite different life habits included in the epifaunal-motile category. While swimmers and facultative swimmers rely on muscular activity for their movements (implying high energy consumption), pseudo-planktonic forms can be regarded as physiologically sedentary. Also, the distances along which they can move are much greater than those attained by swimmers and facultative swimmers [no bivalve has acquired a true nektonic habit (Stanley 1970)]. Having said that, it seems that – at least in this case – all motile forms share a similar extinction pattern, probably due to the similarity they

show. Although pseudoplanktonic forms cannot choose where to go (they may even be moved to potentially lethal environments) their constantly wandering way of life may have allowed them to eventually reach protected environments.

On the other hand, infaunal bivalves show a radiation during Early Mesozoic spurred by mantle fusion and siphon development, acquisitions that enabled them to burrow deeply in the sediment (Stanley 1968) and thus occupy infaunal niches left empty after the P/T extinction in which competition was lower than in epifaunal ones (McRoberts 2001). Bivalves together with brachiopods were the main shelled invertebrates to use both epifaunal and infaunal strategies during earliest Triassic times (Bottjer et al. 2001). At the same time predation pressures [rising due to the Mesozoic Marine Revolution (Stanley 1977)] were less pronounced. Deep burrowers (mainly belonging to the Order Pholadomyoidea) show a slow although almost constantly growing trend in diversity during the Triassic (Ros and Echevarría 2011; Ros et al. 2011), when they did not suffer any major extinction; they can in fact be regarded as positively selected at the T/J boundary. This contradicts the general idea of tiering being seriously affected by mass extinctions (Twitchett 1999). In marine habitats, diverse environmental stresses can differentially affect bivalves and other organisms: wave energy, variations in salinity and temperature, competition for space and resources, predation, etc. (Kauffman 1978; McRoberts 2001). The intensity of most of these factors decreases with tiering, i.e. deep infaunal habitats are buffered against environmental variation if they are compared with epifaunal ones (Kauffman 1978; Roy et al. 2000). In fact, Kauffman (1978) observed that Cretaceous deep burrower species have higher longevities and lower evolutionary rates than species which occupied higher levels in the infauna, and this is fostered by these stress gradients. The deep infaunal habitat could be a refuge, an isolated subenvironment protecting organisms from environmental perturbations. Shallow burrowers (i.e. our shallow infaunal-motile category), on the other hand, are much more prone to suffer these perturbations. As they are usually at some risk of being dug up, they strongly depend on their burrowing ability to survive (many deep burrowers, once they reach their life position, do not need to – and usually cannot – reburrow). Nevertheless, this does not explain the differential extinction they suffer compared to surface-dwelling bivalves.

Among non-motile categories (i.e. attached and sedentary), the extinction pattern also differs. Epifaunal sedentary forms are prone to extinction perhaps due to the high exposure to environmental perturbation. The high depletion on the group is not surprising considering that, in the Rhaetian, this category is almost exclusively constituted by thick shelled megalodontids. While thick-shelled forms

are extinction-prone under certain environmental perturbations (e.g. ocean acidification; Hautmann et al. 2008a), tropical faunas were also more affected by the end-Triassic event (Kiessling and Aberhan 2007a). Attached categories (i.e. cementing, epibyssate and endobyssate) show higher, although negative, diversification rates than the epifaunal-sedentary category (Table 3). Attachment meets the basic bivalve requirement of physical stability. This requirement is commonly achieved through shell thickening in other groups (Stanley 1970), but the attached habit allowed bivalves to establish in turbulent environments (Harper 1991). This habit was attained either by neotenus retention of the byssus (Yonge 1962) or by cementating one valve. This habit could be attained only after the acquisition of the calcitic foliated shell structure (Esteban-Delgado et al. 2008). Many authors agree that predation was an important selective factor acting on these habits, since epifaunal animals are highly exposed. A cementing habit would confer selective advantage by inhibiting manipulability (Harper 1991), while byssate forms tend to be restricted to low-predation habitats due to environmental stress (mostly epibyssate forms) or to stable habitats in which reduced mortality from physical disturbance largely offsets the effects of modern predators (most modern endobyssate forms, Stanley 1977). According to this interpretation, under a biotic crisis, endobyssate forms, although affected by the environmental perturbation, may be somewhat benefited by the reduction of predation pressures. On the other hand, epifaunal-attached habits had higher diversity depletion during the end-Rhaetian event. The epibyssate bivalves are taxonomically varied, since they include some opportunistic (Mytiloidea) and generalised (Arcoidea) taxa, together with more specialised groups (Pectinoidea, Pterioidea), these last ones being more affected than the former ones (Ros and Echevarría 2011). Cementing forms are usually thick-shelled bivalves, and so, like megalodontids, which are expected to be highly affected by ocean acidification. Nevertheless, unlike megalodontids they had a wider paleogeographic distribution; although frequent in the Tethys realm, they are also present in other realms either in the Late Triassic or in the Early Jurassic (Ros 2009), showing higher environmental tolerance. Also, the development of an attached life habit (more stable under physical disturbance) may have helped their survival. As this habit is strongly related to the calcitic foliated shell structure (Esteban-Delgado et al. 2008), it would explain part of the supposed preference on calcitic shell mineralogy.

The CAMP and the selectivity pattern observed among bivalves

Since the synchronicity of the CAMP and the T/J boundary biotic crisis is strongly supported (Hesselbo et al. 2002; Pálffy 2003; Marzoli et al. 2004, although Tanner et al. 2004 discussed the matter), several authors proposed a causal

link between the CAMP volcanism and the T/J mass extinction (Olsen 1999; McElwain et al. 1999; Pálffy et al. 2000; McHone 2003; Pálffy 2003; Whiteside et al. 2010; Ruhl et al. 2011). Kidder and Worsley (2010) suggested that Large Igneous Provinces such as the CAMP triggered the Haline Euxinic Acidic Thermal Transgression episodes that characterise many Phanerozoic mass extinctions according to their model. In order to test this hypothesis, the pattern we found should be able to be explained in this context. Large amounts of CO₂ released into the atmosphere, either directly by outgassing or due to interaction with methane hydrates in the sea floor, would produce global warming by means of a 'greenhouse effect'. In this sense, there is evidence for an increase in partial pressure of CO₂ during the boundary and part of the Hettangian stage (McElwain et al. 1999; Pálffy et al. 2001; Hesselbo et al. 2002; Whiteside et al. 2010; Bonis et al. 2010). The emission of SO₂ could also lead to a climate shift, although in this case it would be a short-term cooling, and also would have important environmental consequences by causing acid rain together with halogen emissions (Pálffy 2003; Tanner et al. 2004), and ocean acidification in addition to that produced by CO₂ (Hautmann et al. 2008a). Volcanism can even cause an excess in productivity by increasing nutrient input, such as iron, into the sea (Pálffy 2003). Related to this last topic, there are many references of high mortality and reduced recruitment among bivalves due to algal blooms (Bricelj et al. 1987; Tracey 1988; Summerson and Peterson 1990; Fiori and Cazzaniga 1999) even in the fossil record (Noe-Nygaard et al. 1987), and most of them are produced by dinoflagellates. It is thus highly suggestive that according to the fossil record and biogeochemical evidence, dinoflagellates experienced an explosive evolutionary radiation during the Late Triassic and Early Jurassic, becoming a prominent primary producer during the Mesozoic (Fensome et al. 1996, 1999). Some recent molecular phylogenetic analyses show that the capacity to produce toxins is scattered along the phylogenetic tree of the group (Zhang et al. 2007). The evolution of this character must have had a devastating impact on marine food chains; if it was already present in Triassic representatives of the group, it would certainly be responsible for many massive mortalities not only among bivalves, leaving many species strongly affected. Although this particular perturbation may have had certain effect in general environmental stress, we found no evidence that these kind of algal blooms produced any differential mortality among various ecological categories of filter feeders.

The environmental stress was not strong enough to affect the relatively protected deep infaunal habitats, but had a strong influence on more superficial ones (epifaunal and shallow infaunal). As explained earlier, endobryonate forms may have benefited by the reduction of predation pressures, somewhat compensating the effects that

environmental perturbations may have had on them, and hence showed positive selection in comparison with other life habits. The motile abilities of swimming and pseudoplanktonic forms might have helped them to avoid many temporary perturbations that would severely affect populations of other ecological categories.

Ocean acidification could have had some consequences on the calcareous shelly faunas, causing the Early Jurassic biocalcification crisis (Hautmann 2004, 2006; Van de Schootbrugge et al. 2007; Hautmann et al. 2008a; Črne et al. 2011). This would explain the high extinction and/or delayed recovery in many massive shelled lineages [megalodontids and oysters (Ros and Echevarría 2011)]. Also, these two taxa (specially megalodontids) had a predominantly Tethyan (i.e. tropical) distribution during the Late Triassic, and tropical bivalve faunas were much more affected by the T/J extinction event than faunas from temperate and cold waters (Kiessling and Aberhan 2007b).

Shallow burrowers are particularly one of the groups whose vulnerability to extinction is hard to explain. One factor reported to have a negative effect on bivalve burrowing behaviour is the presence of heavy metals such as Cd, Cu and Zn among others (Roper et al. 1995; Byrne and O'Halloran 1999; Shin et al. 2002). Leary and Rampino (1990) suggested that the increase in trace metals was a common factor in many mass extinction events; among the different sources, they mention extraterrestrial impacts, volcanism, global wildfires, acid rain and the upwelling of anoxic waters. An example of the potentially devastating effects that heavy metals can produce on the environment is the burrowing bivalve *Mesodesma mactroides* Reeve, which suffered several episodes of massive mortality that left the species on the verge of extinction; the main cause for such mortality (at least in one of the episodes) was the inability of the affected bivalves to reburrow once dug up (Fiori and Cazzaniga 1999). Thompson and Sánchez de Bock (2007) found high values of Cd, Cu and Zn in the bivalves that were killed during the 2004 episode in Argentina, and so they concluded that this mortality event may be a consequence of adverse climatic conditions that dug up the populations combined with a heavy-metal intoxication that altered the physiology of the animals. This could explain the unexpectedly high mortality of this category. Of course the physiology of other categories would be affected too, but it must be borne in mind that it may not be the heavy metal intoxication itself that killed the bivalves but the resultant inability to reburrow. Deep burrowers are rarely dug out, so they had no need to reburrow. Swimmers and facultative swimmers would be strongly affected too, but for this group the inability to move would not be such a problem, since they are epifaunal, and they do not depend so strongly on their motile abilities to regain their life position. For sedentary and attached forms, this physiological problem would not be of great importance,

resulting in lower extinction rates. Of course, massive mortality must not be equated to mass extinction, but episodic massive mortalities related to peaks in heavy metal emissions, may have affected many species of shallow burrowers leaving them much more vulnerable to other perturbations. Heavy metal emissions, as broadly mentioned by Leary and Rampino (1990), may then represent an additional harmful by-product of the CAMP volcanism susceptible of investigation by geologist studying this topic.

Conclusions

- (1) The high value for the extinction rate during the Rhaetian, compared to the mean for the whole Triassic, points to a true mass extinction for bivalves at the T/J boundary.
- (2) At a generic level, there is no difference in extinction proportions between infaunal and epifaunal bivalves at the Rhaetian.
- (3) Genus age at the Rhaetian does not influence extinction risk.
- (4) The apparently negative selection against aragonitic mineralogy seems to be linked to autoecological factors.
- (5) There was a positive selection for deep infaunal-sedentary, shallow infaunal-attached and epifaunal-motile bivalves.
- (6) There was a negative selection against shallow infaunal-motile bivalves.
- (7) Although not statistically significant, the epifaunal-sedentary bivalves show the highest proportional decrease in diversity.
- (8) The selectivity patterns described in this paper are compatible with CAMP caused environmental stress scenario for the T/J boundary mass extinction.

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Note

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