Coping between crises: Early Triassic–early Jurassic bivalve diversity dynamics

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ABSTRACT

The Triassic is bounded by two of the most severe biotic crises, but nevertheless this time was, for bivalves, both a recovery and a diversification period, and a moment to fully exploit some of their evolutionary novelties. Just how and when this was achieved is analyzed in this paper, which covers Induan to Sinemurian bivalve diversity, based on a newly compiled database. Taxonomic diversity and ecospace dynamics are examined separately. Diversity and evolutionary rates were assessed, extinction selectivity was tested using a resampling algorithm, and cohort analysis was used to study extinction patterns. During the Early Triassic most bivalve genera were survivors from the Permian and they were mainly cosmopolitan epifaunal and semi-infaunal endobyssate taxa. Reclined, epifaunal and semi-infaunal bivalves increased in diversity during the Triassic, but from Norian on, their diversity declined, and they were strongly affected by the T/J crisis. Although the Triassic/Jurassic extinction strongly impacted bivalve taxonomic diversity, it had little impact on bivalve ecologic diversity. Not a single bivalve life strategy was eliminated at the end of the Triassic. The present study does not support previous conclusions that infaunal bivalves suffered greater extinction than epifaunal ones during the T/J extinction. Not all life strategies were equally affected by the extinction event, being the deep infaunal burrowers positively selected. Bivalves with major energetic requirements seem to have been more affected with negative selectivity on fast shallow burrowers. The ecologic diversity changes of bivalves during the Late Triassic and several adaptations of durophagous predators reflect the effects of increasing predation pressure and support a Late Triassic origin of the Mesozoic Marine Revolution.

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1. Introduction

Bivalves are a highly diversified molluscan class, with a long history dating from Early Cambrian times (Cope, 2000). Although the group already showed a steady diversification trend during the Paleozoic, it only became highly successful and expanded rapidly from the Mesozoic onwards. The Triassic was, for bivalves, first a recovery period and later a biotic diversification time. It was also the time when bivalves first fully exploited some of their evolutionary novelties.

The Triassic was bounded by two severe biotic crises: the P/T and T/J, both of which are included in the "big five" extinction events, which had devastating effects on a global scale (Newell, 1967; Raup and Sepkoski, 1982). The P/T extinction event was the most severe biotic crisis in the history of life on Earth (Raup, 1979; Raup and Sepkoski, 1982; Erwin, 1993, 2006), not only in terms of taxonomic losses but also in terms of the drastic re-organization of marine ecosystems (Erwin, 2006; Wagner

et al., 2006). The subsequent recovery of ecosystems was slow compared with other extinction events (Erwin, 1998), and did not end until Middle Triassic times (Erwin, 1993; Benton, 2003). The P/T extinction did not affect bivalves to the same degree that it affected many other marine invertebrate groups (Yin, 1985; Erwin, 1993). Furthermore, during the Triassic, bivalves underwent an extraordinary evolutionary radiation due, in part, to mantle fusion and siphon development (Stanley, 1968), which allowed them to develop infaunal niches previously poorly exploited by both bivalves and brachiopods during the Paleozoic.

From a paleoecologic viewpoint, bivalves (together with brachiopods, although the latter were disproportionally decimated) were the main shelled invertebrates to use both epifaunal and infaunal strategies during the P/T post-crisis (Bottjer et al., 2001). Bivalves became the dominant shelled marine invertebrates in benthic communities during the earliest Triassic, replacing the role previously played by brachiopods (Fraiser and Bottjer, 2007), although their abundance had already considerably increased during the late Permian (Clapham and Bottjer, 2007). A bivalve diversification phase began during the Anisian (early Middle Triassic) and continued into the Late Triassic, when extinction played once more an important role (McRoberts, 2001; Ros, 2009; Ros and Echevarría, in press). The T/J extinction event was less important than the previous one and, according to Bambach et al. (2004) and Lucas and Tanner

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(2008), it unfolded during the entire Late Triassic and was the result of high extinction and low origination rates (but see Alroy, 2008), although this pattern is not evident for bivalves (Ros and Echevarría, in preparation). On the other hand, Hallam (1981, 2002) recognized a single extinction event at the end of the Triassic. The earliest Jurassic saw a new biotic recovery period which, although not as well studied as the Triassic one, was apparently faster. Already during the Hettangian, the initial stage of the Jurassic, significant diversification is observed among marine invertebrates, culminating during the Pliensbachian, middle Early Jurassic, with the reappearance of reef organisms (Hallam and Wignall, 1997).

During post-Paleozoic times there were great changes in marine communities triggered by predator diversification and the co-evolution of defensive and evasive adaptations in their prey (Vermeij, 1977). The Triassic is a key stage to study bivalve taxonomic and ecologic diversity because it is the time when all these changes became evident. Predation pressure increased significantly only since the Early Cretaceous, when predators became both abundant and diverse (Vermeij, 1977; Kowalewski et al., 1998); however, its effects were already evident during the Late Triassic (e. g. Hautmann, 2004b; Harper, 2005).

This paper deals with some significant topics related to the evolution of bivalve diversity from the beginning of the Mesozoic. We cover the time interval from just after the P/T extinction (Induan, earliest Triassic) to the T/J recovery in the Sinemurian (Early Jurassic). We will deal not only with taxonomic diversity dynamics, but also with the evolution of bivalve ecospace during this period, with special emphasis on the T/J extinction and its selectivity and the bivalve infaunalization observed during the Late Triassic (McRoberts, 2001) and later times (Aberhan et al., 2006). The relation of infaunalization to the Mesozoic Marine Revolution (Vermeij, 1977) will also be addressed. Two sorts of data can help to identify potential bivalve predators in the past: predation marks and morpho-functional study of both predators (in search of structures indicating molluscivory) and preys (exploring for likely defensive structures or behavior) (Vermeij, 2002). Of all possible predation methods (see Vermeij, 1987; Harper, 2003) we will concentrate on crushing and drilling, since these are the only ones which leave direct evidences in the fossil record, unlike whole ingestion or prying (Harper, 2005).

2. Data and methods

2.1. Database

Our primary data source is Ros (2009, summarized in p. 366–374), freely available on-line 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 is a new worldwide stage-level compilation of marine bivalve genera, following a coherent systematic scheme, and contains information on stratigraphic range, paleogeographic distribution, autoecology, and shell mineralogy for all marine bivalve genera during the Induan–Sinemurian interval. Species of each genus were carefully revised and the diverse systematic interpretations different authors made for some of them were critically taken into account. An example can illustrate this database feature: 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. Data were compiled from all available literature containing descriptions and/or illustrations of bivalves for this interval in order to check generic assignments where needed. Also, expert advice on different subgroups or specific geographic areas was sought whenever necessary.

The unit employed 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 (e.g. Raup and Stanley, 1978; Jablonski et al., 2003), in many cases subgenera were proposed based on criteria later regarded as specific level criteria. Families Entoliidae or Halobiidae provide good examples (Ros, 2009). In the family Halobiidae only four genera were included in the database: *Halobia*, *Aparimella*, *Daonella* and *Enteropleura*. Many other genera and subgenera were proposed (*Perihalobia*, *Zittelihalobia*, *Indigirohalobia*, *Primahalobia*, *Comatohalobia*, *Magnolobia*, *Moussonella*, *Grabella*, *Arzelella*, *Loemmelella*, *Pichlerella*) but their diagnostic criteria are regarded of specific level (see McRoberts, 1993, 2000; Campbell, 1994; see also discussion in Ros, 2009, p. 195). Similarly, in family Entoliidae there is no consensus among workers about the taxonomic criteria at different levels and sometimes they clearly use specific criteria and even superficial shell structures easily influenced by taphonomic processes, to diagnose at a generic level (Johnson, 1984; Damborenea, 2002; see also discussion in Ros, 2009, p. 221). The use of subgenera in order to minimize the "Pull of the Recent" (Raup, 1972, 1978) is not necessary in this case, since no stratigraphic range was extended in the analyzed time interval because of the presence of an extant species.

Genera were assigned to families following Cox et al. (1969) and more recent literature, when available. We follow the systematic arrangement by Amler (1999) and Amler et al. (2000) with some modifications discussed in Ros (2009).

We used Gradstein and Ogg (2004) Geologic Time Scale for absolute ages. Although the Triassic time scale is still unstable (Schultz, 2005) since most boundary stages lack a definite Global Standard Section and Point (GSSP), Ros data base (2009) 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 future, the database will still be as robust as those absolute ages. Different time scales in the analyzed papers were updated using the conversion tables in Paleobiology Database (PBDB; http://paleodb.org) and GeoWhen (http://www.stratigraphy.org/geowhen/index.html). A special problem was the stratigraphic provenance of Norian and Rhaetian faunas in papers published between Tozer (1979), who initiated the tendency to 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 the 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 time ranges used here are observed ranges defined by first appearances (FADs) and last appearances (LADs), and are therefore only proxies for actual origination and extinction times. Sample biases, stratigraphic gaps, regression and transgression effects, and many other factors can affect first and last appearances (Holland, 1995). Besides, it should be remembered that bivalve temporal ranges are especially influenced by lithologic facies.

Paleoecologic data were framed, with some adjustments (discussed later) into Bambach et al. (2007) ecospace, which considers three main factors: relationship with the water column/substrate, feeding type, and degree of motility/fixation. Each genus was assigned to a living strategy (see Table 1 and Appendix A). Taxonomic data were also classified according to relation with the substrate (epifaunal or infaunal). Endobyssate, semi-infaunal bivalves were grouped with infauna, whereas free lying bivalves with heavy shells and semi-infaunal habits (e.g. some megalodontids) were grouped with epifauna.

2.2. Methods

2.2.1. Assessment of diversity and evolutionary rates

In order to analyze diversity changes we used the Boundary Crossers (BC) metric (Sepkoski, 1979; Foote, 2000) as estimator, since it is a precise measure of the taxa present at a time point (the top of the stage),

Table 1
Ecologic categories for tiering, motility level and feeding mechanism recognized here for bivalves. The main differences with the invertebrate ecospace of Bambach et al. (2007) are: 1) only four tiering categories are considered because no bivalves with pelagic or erect mode of life are known; 2) motility level: the two first categories only include burrowing bivalves because they are the only ones that can move continuously, and the other four categories are always for epifaunal or semi-infaunal bivalves; 3) feeding mechanism: only two categories are considered because no other mechanisms are inferred in bivalves from the study time interval. (Modified from Bambach et al., 2007).

Category	Description
Tiering	
Epifaunal	Benthic, living above substrate/water interface
Semi-infaunal	Partly infaunal, partly exposed to the water column
Shallow infaunal	Infaunal, living in the top 5 cm of the substrate
Deep infaunal	Infaunal, living more than 5 cm deep in the substrate
Motility level	
Fast motile	Fast burrower
Slow motile	Slow burrower
Facultative, unattached	Reclined free-lying with ability to swim
Facultative, attached	Byssate with ability to swim or pseudoplanktonic
Non motile (sedentary), unattached	Not capable of self-propulsion, free-lying, reclined
Non motile (sedentary), attached	Not capable of self-propulsion, attached (cemented or byssate)
Feeding mechanism	
Suspension feeder	Capturing food particles from the water
Deposit feeder	Capturing loose particles from the substrate

and the Mean Standing Diversity (MSD) as estimator for comparisons of diversity among some groups (Foote, 2000; Hammer and Harper, 2006). Diversity is recorded as generic richness. To standardize the origination and extinction rates MSD was used summing all the continuous ranges (Cr), one half for each LAD (L) and FAD (F) (Foote, 2000) and one third for each singleton (S) (Hammer, 2003; Hammer and Harper, 2006).

$$BC = Cr + F \qquad MSD = Cr + L/2 + F/2 + S/3$$

Origination rate (O_r) was calculated as number of FADs (including singletons) divided by MSD and standardized by the length of the stage, while extinction rate (E_r) was obtained as LADs (including singletons) divided by MSD and also standardized by the length of the stage (Δt) (Van Valen, 1984); diversification rates (D_r) were calculated by the subtraction of extinction rate to origination rate (Sepkoski, 1978).

$$Er = L + S/MSD \times \Delta t \qquad Or = F + S/MSD \times \Delta t \qquad Dr = Or - Er$$

The MSD data are plotted at the mid points of the stages, whereas the BC data are plotted at the top of each stage because while the BC is an actual metric of the diversity at one time-point (at the end of the stage), the MSD is a standardized estimation of the diversity for a whole stage. Taking into account that it is better to refer the rates to similar time intervals (Sepkoski, 1981), we combined the two Lower Triassic stages (Induan and Olenekian). Error bars in extinction and origination rates represent 95% confidence intervals (equivalent to ± 2 standard errors). In the analysis of extinction selectivity, singletons and first originations were always included.

2.2.2. Extinction selectivity

To statistically test for ecologic selectivity in the T/J extinction, we used a resampling algorithm to test if the number of extinct genera in each ecologic strategy was significantly higher or lower than would be expected under random extinction. We randomly drew 55 genera (extinct at the end of the Rhaetian) without replacement from the total genera pool (127 genera) to generate an expected distribution of the number of extinct genera inside each strategy (see Fig. 1). For this analysis an R code was developed (R Development Core Team,

2008) by Javier Echevarría (La Plata Museum, Argentina). In order to test for the reliability of the code, we repeated the analysis but sampling the survivor instead of the extinct genera, obtaining similar values. The number of iterations was 10,000. 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 tail test (we were looking for significantly higher or lower values than those expected by chance).

2.2.3. Cohort analysis

In order to study the extinction pattern, we used cohort analysis (Raup, 1978, 1987). This procedure consists in calculating the survivor data of a cohort of taxa. A cohort is the group of taxa which originated at a given moment of geologic time, by analogy with organism cohorts of a population in ecology. The method consists in linking percent points of surviving taxa for specific times by broken lines, and this is represented in a semilogarithmic graph of geologic time/proportion. The alignments, always with negative slope, provide a qualitative image of extinction rates and allow to comparing them and following their fate until Holocene. Nine cohorts are considered in the study interval (Induan to Sinemurian).

3. Some taphonomic considerations

Evolutionary readings of the fossil record should be preceded by a consideration of the taphonomic factors that can distort or disguise interpretations of paleobiologic processes (De Renzi, 1992). Shell mineralogy, shell size, and even the scale of geographic and stratigraphic sampling, among other traits, can potentially compromise interpretations of the fossil record.

3.1. Shell mineralogy

The effect of rarefaction by geologic age must also be considered, and this probably affects the more ancient fossil record (Raup, 1976a, 1976b; Raup and Stanley, 1978; De Renzi, 1992). Rarefaction by age can produce bias against aragonitic shells, and this bias could potentially influence the Triassic fossil record (De Renzi and Ros, 2002; Ros and De Renzi, 2005). Bivalve shells can be entirely aragonitic, calcitic except for aragonitic myostracal (muscle scar) and ligament mineralization, or any proportion of aragonite and calcite in the major shell layers (Carter, 1990). The differential solubility of aragonite and calcite (Kern and
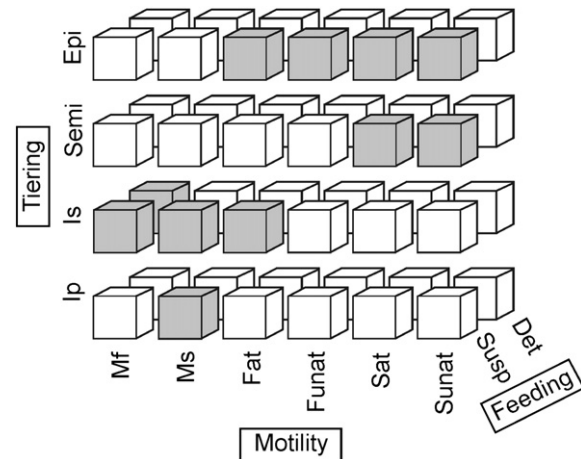

Fig. 1. Theoretic bivalve ecospace during the Induan–Sinemurian interval defined by the three variables (with their categories): tiering (Epi, Semi, Is, Ip), motility level (Mf, Ms, Fat, Funat, Sat, Sunat) and feeding strategy (Susp, Det). The strategies occupied by bivalves are shaded. Susp: suspensivorous; Det: detritivorous; Epi: epifaunal; Semi: semi-infaunal; Is: shallow infaunal; Ip: deep infaunal; Mf: fast motile; Ms: slow motile; Fat: facultative attached; Funat: facultative unattached; Sat: sedentary (non motile) attached; Sunat: sedentary (non motile) unattached.

Weisbrod, 1964; Rolfe and Brett, 1969; Morse et al., 1980; Kidwell, 2005) can result in underestimation of aragonitic bivalve diversity (Harper, 1998; Bush and Bambach, 2004; Ros and De Renzi, 2005; Valentine et al., 2006). Inorganic calcite is 35% less soluble than aragonite, but other factors, such as crystal size and shape (Harper, 2000; Valentine et al., 2006) and the amount of organic matter (Harper, 2000) can also influence solubility. However, Kidwell (2005) did not find a significant mineralogic effect on estimates of family-level bivalve diversity in the fossil record. The plesiomorphic condition in the Bivalvia is entirely aragonitic shells. Bivalves are here divided into two categories: aragonitic and bimineralic. Bivalves with even a thin calcitic outer shell layer, such as many Paleozoic pterioids and pectinoids, were classified as bimineralic because such a layer increases their preservation potential. As shown in Fig. 2, aragonitic bivalve families were proportionally more abundant during the early and middle Paleozoic, but bimineralic families became nearly as abundant during the Permian. This figure also shows that aragonitic families increased at a more rapid pace than the bimineralic ones throughout the Mesozoic although they may be underrepresented (Ros and De Renzi, 2005). Wright et al. (2003) compared two associations from similar offshore settings in the Lower Jurassic of South Wales: a typical fossil assemblage and an assemblage where the early silicification preserved a more complete shelly biota. They found that the nonsilicified assemblage is dominated by calcitic and bimineralic epifaunal and semiinfaunal bivalves while the aragonitic infaunal bivalves are rare. On the other hand, in the silicified assemblage although other bivalves are abundant too, the aragonitic shallow burrowers are clearly dominant (see Fig. 2 in Wright et al., 2003). This study demostrated that diversity observed during Mesozoic may be biased in favor of calcitic bivalves by early dissolution of aragonite and this fact can distort our diversity estimations.

3.2. Substrate relationship and shell size

Relationship to the substrate apparently does not influence family-level diversity estimates in the fossil record (Harper, 2000; Ros and De Renzi, 2005), but there seems to be a negative bias against smaller bivalves (Cooper et al., 2006). This is a serious problem while analyzing diversity just after extinction, since organisms tend to be smaller during

Fig. 2. Diversity of bivalve families according to shell mineralogy. C: Cambrian, Or: Ordovician, Si: Silurian, Dv: Devonian, Cb: Carboniferous, Pm: Permian, Tr: Triassic, J: Jurassic, K: Cretaceous, Cz: Cenozoic.
(Modified from Ros and De Renzi, 2005).

survival and recovery stages (the "Lilliput effect"; see Twitchett, 2006). Bivalve diversity could therefore be underestimated for the Early Triassic because of this bias (Hautmann and Nützel, 2005).

3.3. Geographic and stratigraphic range

Geographically restricted taxa are more likely to be overlooked in the fossil record, thereby leading to underestimations of diversity (Valentine et al., 2006; Ros, 2009). The same applies to taxa with more restricted stratigraphic ranges: the longer the stratigraphic range, the more likely a taxon is to be recorded. Furthermore, time and geographic range appear to be positively correlated (Miller and Foote, 2003; Foote et al., 2008).

4. Results

4.1. Induan–Sinemurian taxonomic diversity dynamics

4.1.1. Standing generic diversity

Total bivalve generic diversity steadily increased from the Induan (earliest Triassic) to the Norian (Late Triassic) (Fig. 3A). The total number of genera then diminished through T/J and then rose again during the Lower Jurassic. Generic first appearances (FADs) reached a maximum in the Carnian (63 genera), then diminished to a minimum during the Rhaetian (Fig. 3B). The trend of last appearances (LADs) follows that of FADs from Induan to Norian, but differs from FADs by peaking in the Rhaetian (Fig. 3B). Not all bivalve orders contributed equally to this diversity change (Fig. 4). Pectinida, Pteriida, Venerida and Trigoniida are the most diverse orders during the study interval. Pectinida and Pteriida are mostly epifaunal bivalves, were well represented in the Paleozoic and reached a diversity peak during the Norian, with a slight decrease from then on. Other, mainly infaunal orders, such as Venerida, progressively increased in generic diversity through the entire interval, with no significant decrease at the T/J boundary. The Trigoniida also increased during all of the Triassic then clearly declined in generic diversity at the T/J boundary.

When infaunal and epifaunal bivalves are analyzed separately (Fig. 3A), epifaunal generic diversity is slightly greater than infaunal diversity until the Carnian, when both lines intersect, and from then onward to the present, infaunal bivalves were always more diverse than epifaunal ones. Note that the diversity of epifaunal and infaunal bivalves decreases in parallel, with infaunal diversity remaining greater than epifaunal diversity. During the study interval, generic diversity climaxed during the Norian. The diversity of each group declined after its maximum until the end of the Rhaetian.

4.1.2. Origination, extinction and diversification rates

Origination rates during the Triassic show an overall diminishing trend (Fig. 5A) with two successively lower peaks (Anisian, Carnian), then decreasing from the Carnian to a minimum in the Norian. The origination rate then rose slightly in the Rhaetian and again in the Hettangian in the recovery from the T/J extinction. The origination rate was greater for epifaunal taxa during Lower and Middle Triassic, however infaunal generic origination rates were greater than epifaunal ones from the Carnian onwards. During the Hettangian, although both infauna and epifauna show a peak, origination rates were significantly greater for the infauna (0.1063 versus 0.053; Fig. 5B and C).

Concerning extinction rates during the Triassic three peaks are observed: one during the Lower Triassic (Induan + Olenekian), other during Carnian and another, greater, during the Rhaetian. In the Early Triassic the greater extinction was for epifaunal bivalves and the same is observed for the entire study interval except in Ladinian, Norian and Rhaetian, when the rates were very similar in the two collectives. The Early Triassic value was only exceeded in Rhaetian times, when as many as 53 genera disappeared (42%). In the Anisian and Carnian, the generic extinction rate was particularly severe for epifaunal taxa (0.0477
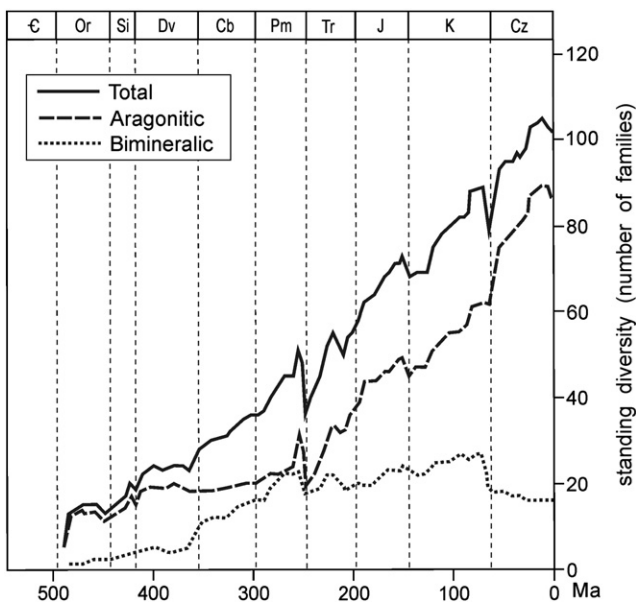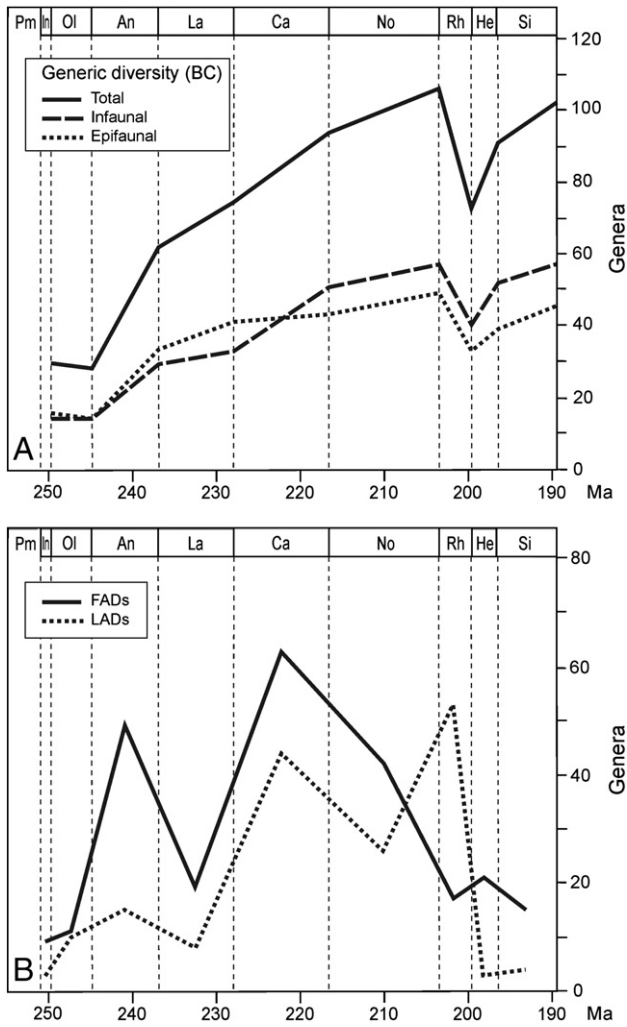
and 0.0529, respectively), almost all genera of this group were singletons. The extinction rates were similar for both collectives during the T/J event (0.1304 and 0.1391) (Fig. 5B and C).

Within the Triassic, the Carnian was characterized by a greater diversification rate for infaunal genera (0.0342) relative to epifaunal genera (0.0037) (Fig. 5B). The generic diversification rate was positive during the Triassic except around the T/J boundary, when a negative value is observed, with epifauna declining faster than infauna due to a greater origination rate of this collective during Rhaetian. During the Hettangian, infauna generic diversification rates (0.0921) were far greater than for epifauna (0.0441).

The Carnian stage was a time of inflection, when epifaunal bivalves showed higher extinction and lower origination rate relative to infaunal ones, and obviously lower diversification rate, and this trend went on during the rest of study interval (Fig. 5C).

4.1.3. New taxa

The previous analyses indicate that one of the most significant events in the history of Triassic–Early Jurassic bivalve diversity was the change from an epifauna-dominated to an infauna-dominated fauna (Fig. 3A). Considering only the genera with Induan to Sinemurian FADs, infaunal bivalve diversity greatly exceeded that of epifaunal bivalves from Carnian times onwards, and the survivorship of infaunal bivalves was greater than the epifaunal collective mainly for Lower Jurassic genera (Fig. 6A and B).

At a closer look, when the fate of stage-delimited cohorts of bivalve genera originating in the Triassic is examined (Fig. 7A, B and C), it is evident that the Early and Middle Triassic cohorts were more stable, with the exception of the Olenekian cohort, which underwent three extinction events, at T/J boundary, in the Late Jurassic, and in the Early Cretaceous (Fig. 7A and B). After steadily diminishing throughout the Triassic, the Anisian and Ladinian (Middle Triassic) cohorts suffered no major losses until the K/T extinction (Fig. 7B). In contrast, the Late Triassic (Carnian, Norian, and Rhaetian) cohorts show more pronounced decay during the Jurassic and the Cretaceous, culminating in heavy losses during the K–T extinction (Fig. 7C). The differential success of the earlier and later Triassic generic cohorts may reflect the progressive biotic filling up of ecospace, with a parallel increase in competition (De Renzi and Ros, 2004; Hautmann, 2007), and the resultant progressive increase in origination rates of stenocore genera, with smaller geographic distributions and shorter durations (Ros, 2009). Interestingly, the Hettangian and Sinemurian (Early Jurassic) generic cohorts show an intermediate
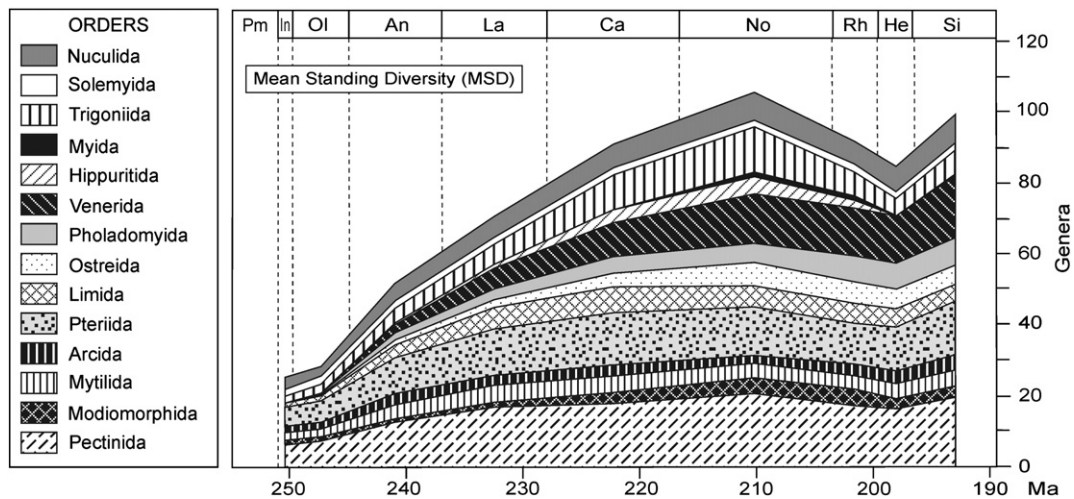
Fig. 3. A. Bivalve generic diversity (BC) during the Induan–Sinemurian for infaunal, epifaunal and all life strategies. B. Bivalve first appearences (FADs), and last appearences (LADs) during the Induan–Sinemurian.
(Modified from Ros, 2009).

Fig. 4. Generic diversity (MSD) of bivalve orders during the Induan–Sinemurian interval. In the Hippuritida, all Triassic genera went extinct at the T/J boundary but the order reappeared in the Sinemurian with *Pachyrisma*.
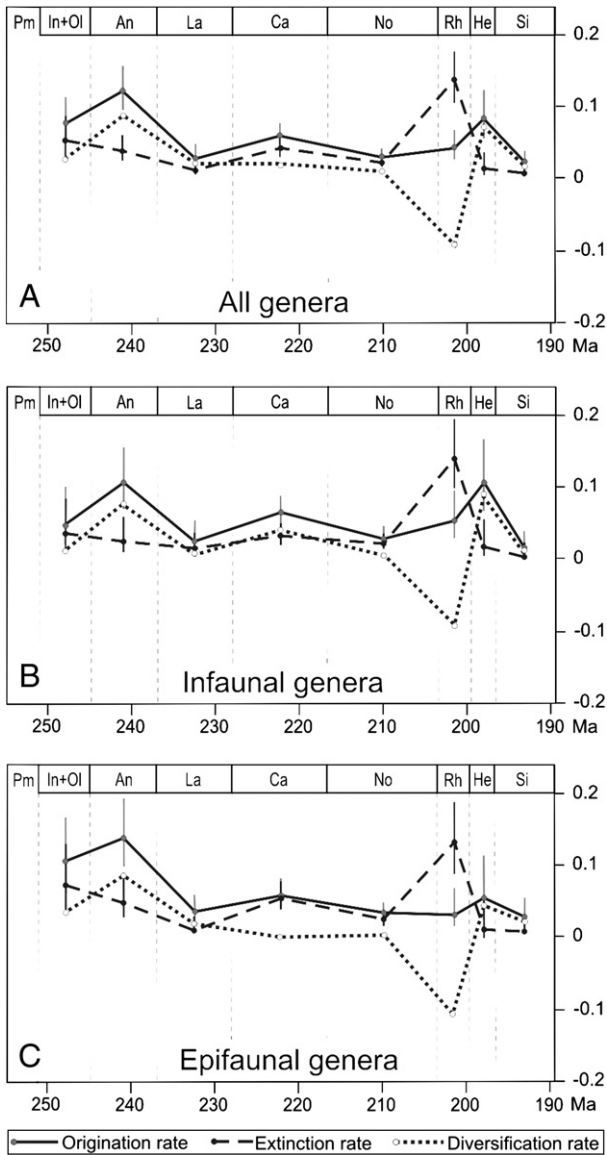Data from Ros (2009).

Fig. 5. Bivalve evolutionary rates for the Induan–Sinemurian interval. A. Total bivalve genera; B. Infaunal genera (infaunal and endobyssate semi-infaunal); C. Epifaunal genera (epifaunal and reclined semi-infaunal). Error bars represent 95% confidence intervals.
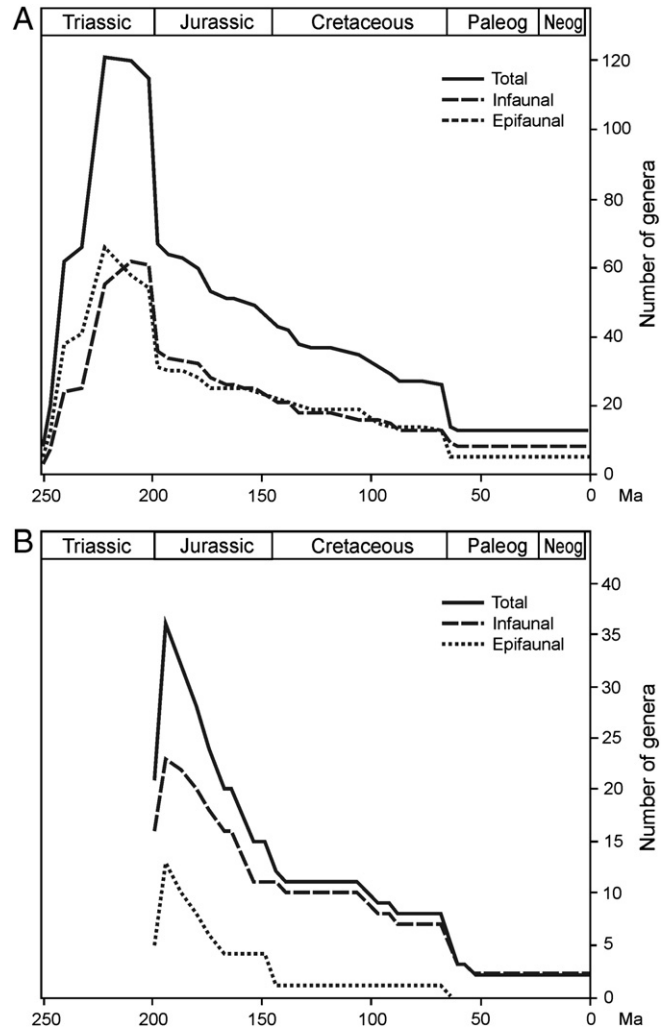Data from Ros (2009).

Fig. 6. A. Bivalve genera originating during the Triassic (Induan–Rhaetian) and their fate since the Pliensbachian times. B. Bivalve genera originating during the Hettangian and Sinemurian (Early Jurassic), and their fate since the Pliensbachian.
Data and figures from Ros (2009).

stability between that of the Lower and Upper Triassic cohorts, comparable to the Middle Triassic cohorts (Fig. 7D). This may reflect the different intensity of the P/T and T/J extinction events. This pattern agrees with the observation by Miller and Foote (2003) that marine post-Paleozoic taxa originating during recovery periods tend to persist longer than others. During the Triassic the greatest longevities are observed in genera which originated after P/T crisis, during Early Triassic, and, after T/J crisis, during Hettangian (Fig. 8). The lowest longevities are those of genera originated during the Carnian, the Triassic stage with major diversification and turnover, when a lot of singleton genera flourished.

4.2. Induan–Sinemurian bivalve ecospace dynamics

Much has been written about long term changes in the use of ecospace by marine invertebrates, especially in relation to the decline of the Paleozoic fauna and the rise of the Modern fauna (Bambach, 1983; Bottjer et al., 1996; Clapham and Bottjer, 2007). Such analyses can help identify the traits that have been important in bivalve

evolutionary dynamics, and perhaps point to ecologic factors during the T/J extinction. We analyzed bivalve ecospace utilization during the Induan–Sinemurian interval.

4.2.1. Triassic–Early Jurassic bivalve ecospace categories

The ecospace categories used here for the Triassic and Early Jurassic are: tiering (epifaunal, semi-infaunal, shallow infaunal, deep infaunal), motility level (fast motile, slow motile, facultative attached, facultative unattached, sedentary attached, sedentary unattached), and feeding strategy (suspensivorous, detritivorous) (Table 1). These categories differ slightly from those proposed by Bambach et al. (2007) for all marine animals, and from the so-called *Bambachian megaguilds* of Droser et al. (1997). Bambach et al. (2007) divided ecospace by feeding type, degree of mobility or attachment, and tiering. Instead, we use only four tiering categories because no Triassic or Early Jurassic bivalves with pelagic or erect life habits are known. Also, our motility category is restricted to burrowers and swimmers (with swimmers and pseudoplanktonic regarded as facultative motile) in relation to epifaunal and infaunal strategies, and our feeding category is restricted to suspensivorous and detritivorous. Carnivorous bivalves (e.g., Septibranchia) did not appear until the Middle Jurassic. Burrowing motility is here divided into fast and slow, as suggested by shell morphology (discussed in Ros, 2009), but fast-burrowing bivalves probably did not diversify until the Cenozoic (Checa and Jiménez-Jiménez, 2003), although *Tancredia* is
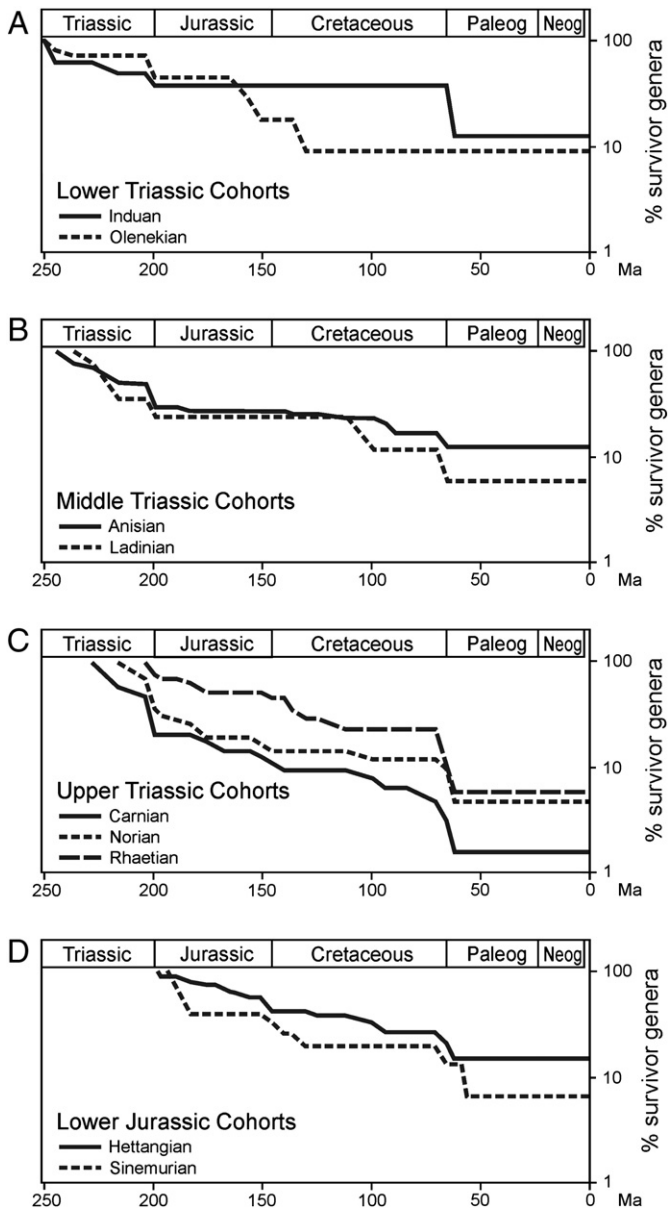
Fig. 7. A. Bivalve genera originating during the Early Triassic and their subsequent fate. B. Bivalve genera originating during the Middle Triassic and their subsequent fate. C. Bivalve genera originating during the Late Triassic and their subsequent fate. D. Bivalve genera originating during the Early Jurassic (Hettangian and Sinemurian cohorts) and their subsequent fate.
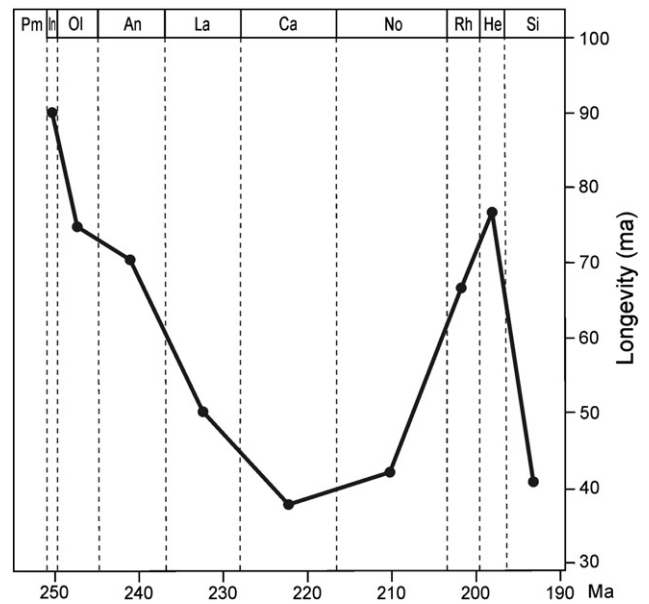Data and figures from Ros (2009).

Fig. 8. Median longevity (duration of the taxon in the geologic record, counted in millions of years) of genera originated in each stage of the study interval.

regarded as a fast burrower (Stanley, 1977a) and probably had an Early Jurassic origin (Ros, 2009). Some bivalves change their mode of life during ontogeny, but in this analysis only adult life habits are considered.

In order to examine trends in ecospace utilization among Induan–Sinemurian bivalves, we recorded the boundary crossers estimate of diversity by stage representing each life habit category (see Fig. 1, for details see Appendix A).

4.2.2. Variations in ecospace utilization

All life strategies followed by Induan bivalves were already occupied during the Permian. Therefore, Induan ecologic biodiversity reflects only the life strategies persisting after the P/T crisis. The best represented of these is suspensivorous, epifaunal, sedentary attached taxa, most of which were epibyssate (Fig. 9A–B). The epibyssate, endobyssate

semi-infaunal and shallow burrowing life habits (comprising several ecospace categories) were the most diverse life strategies during the Induan stage. The cemented mode of life is represented during Induan times only by *Pegmavalvula*, survivor of P/T crisis but which did not survive into the Middle Triassic (Newell and Boyd, 1995). However, cemented genera subsequently diversified in the Middle and Late Triassic when epibyssate genera decreased in diversity (Fig. 9B).

During the Olenekian stage, two Permian life strategies re-appeared: deep burrowers, represented by *Pleuromya*, and epifaunal, sedentary, unattached bivalves represented by *Bositra*. Bivalves using the former strategy became increasingly diverse during the Triassic and Jurassic, and they were only barely affected by the end-Triassic extinction (1 genus lost) (Fig. 9E). However, epifaunal, sedentary, unattached bivalves peaked during the Norian, were reduced in generic diversity during the Rhaetian, and then remained roughly constant to the Sinemurian (Fig. 9A). The reclining mode of life, including free epifaunal and semi-infaunal sedentary unattached forms, increased in diversity up to the Late Triassic (Fig. 9A and F), semi-infaunal bivalves reached a maximum in the Norian, only to disappear altogether at the end of the Rhaetian (all Triassic forms). Nevertheless, the latter strategy was resumed in the Hettangian by *Weyla* and in the Sinemurian by *Weyla* and *Pachyrisma*.

During the study interval, endolithic bivalves first appeared in the Late Triassic, probably in the Norian with the genus *Lithophaga* (Kleemann, 1994). They are here gathered with deep burrowers because deep infaunal habitat and boreholes produced by endolithic activity are both "safe places". At the Carnian, also sedentary infaunal attached (endobyssate) genera first appeared, as represented by some Kalenteridae and Carditidae which probably could burrow but spent almost all their lives as endobyssate. However, the latter strategy was apparently not very successful just after the Rhaetian, being occupied in the Hettangian and Sinemurian by only one genus, *Kalentera* (Fig. 9D).

Among infaunal bivalves, the most successful strategy seems to have been suspensivorous, shallow burrowers, although this was severely reduced by the end-Triassic crisis (Fig. 9C–D). Detritivorous were always less abundant than suspensivorous during the study interval (Fig. 9C) but they had a more stable trend, as in all their history (Skelton et al., 1990). Fast burrowers (either suspensivorous or detritivorous) were more seriously impacted by the T/J extinction than slow burrowers (Fig. 9C–D).
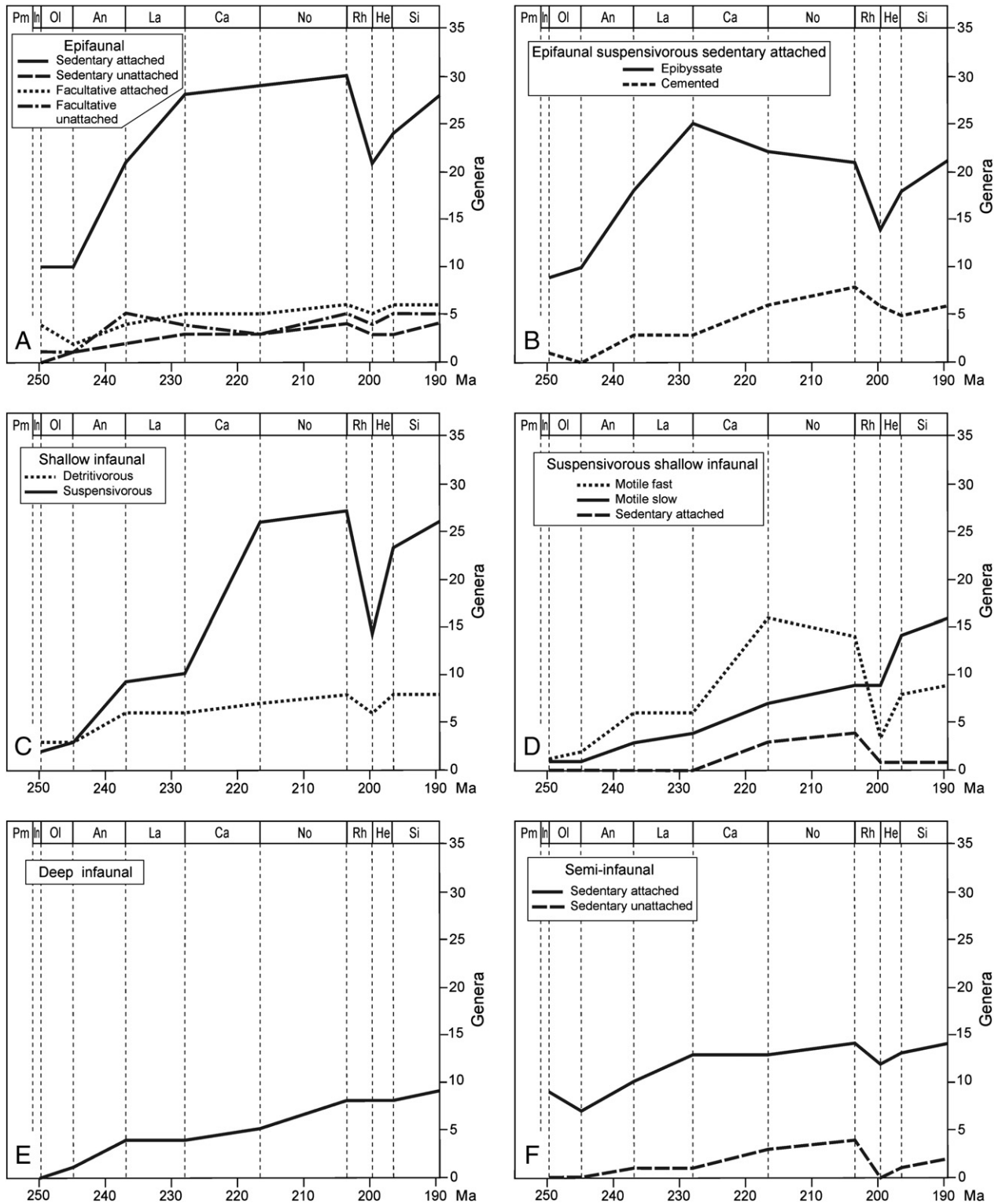
Fig. 9. Ecospace occupied by Induan–Sinemurian bivalves. The generic diversity (BC) corresponding to each life strategy is shown by stage. A. Epifaunal. B. The suspensivorous, epifaunal, sedentary (non-motile), attached strategy decoupled in terms of cemented and epibyssate animals. C. Shallow infaunal. D. Suspensivorous shallow infaunal. E. Deep infaunal. F. Semi-infaunal.

4.2.3. Tiering

During the P/T extinction, epifaunal tiering considerably decreased in soft bottom suspensivorous communities (Bottjer and Ausich, 1986; Bottjer et al., 1996; Ausich and Bottjer, 2001). Infaunal tiering also declined, at least in the equatorial realm (Knaust, 2010), and this is coincident with the absence of deep infaunal burrowers during Induan times. Nevertheless, infaunal tiering rapidly recovered to Permian levels and was not affected by the T/J extinction (Ausich and Bottjer, 2001) (Fig. 9E). Deep infaunal was for bivalves one of the most stable ecologic categories during the study interval. The

reestablishment of tiering is a good measure of recovery after extinction (Twitchett, 1999), and during the Anisian (Middle Triassic), deep burrowing bivalves re-appeared and diversified.

Bivalves occupy only the lowest levels of epifaunal tiering, but they can be secondary tierers, using skeletons of primary tierers to lift themselves above the substrate, thereby reaching elevations up to 20 cm (Bottjer and Ausich, 1986). Cemented and occasionally swimming byssate bivalves increased throughout the study interval (Figs. 9A–B and 10). In comparison with brachiopods, which throughout the entire Phanerozoic developed only very slight infaunal tiering (between −6 cm and +5 cm; Bottjer and Ausich, 1986), bivalves came to occupy the deepest infaunal levels, up to 100 cm (Ausich and Bottjer, 1982) due to siphon development (Stanley, 1968, 1977a). Hence, Triassic bivalves occupied tiering categories vacated during the Early Triassic, whereas brachiopods remained in tiering categories that were never vacated, and which were therefore characterized by intense competition from other marine invertebrates.

4.2.4. Triassic/Jurassic extinction selectivity: autoecologic and shell mineralogic traits

The statistical significance of extinction selectivity was tested using a resampling algorithm for each ecologic strategy. In the case of tiering and motility, the number of extinct was found to be lowest for deep infaunal bivalves ($p = 0.02$) and in the limit of significance, highest for epifaunal and semi-infaunal, sedentary free bivalves ($p = 0.04$) (Table 2A). When examining all ecologic strategies, the number of extinct genera was greatest for reclined, semi-infaunal bivalves ($p = 0.01$; 100% of Triassic genera became extinct, although the group suffered a pseudoextinction (Allasinaz, 1992); Fig. 11), and fast motile shallow infaunal bivalves ($p = 0.006$), and was lowest for deep infaunal bivalves, at the limit of significance ($p = 0.03$; only one genus disappearing at the T/J boundary, i.e., 11%; Fig. 11) (Table 2B).

Due to the increased interest in this trait during the last years (Hautmann, 2004a, 2006 but see also Kiessling et al., 2007 and Mander et al., 2008 for a discussion) and its relation with life habit (infaunal and epifaunal), shell mineralogy was included in the analysis. In this case a chi-square test was applied because only two categories are considered: aragonitic (all shell layers composed by aragonite) and bimineralic (at least one of the shell layers is composed by calcite). Wholly aragonitic bivalves suffered proportionally more extinction than bimineralic ones during T/J event although no differences are detected by Chi-square test ($\chi^2 = 2.9874$, $p = 0.084$) (Fig. 12A). Since this character is strongly correlated with the life habit, as all infaunal bivalves are aragonitic, a particular analysis was also

Table 2
Results of the resampling analysis of the autoecologic traits showing the proportion of iterations that resulted in the same or lower number of observed extinctions and the proportion of iterations that resulted in the same or higher number of observed extinctions. Significant values in bold ($p < 0.025$). Key to abbreviations in Fig. 1. A. All ecologic strategies. B. Ecologic strategies grouped taking into account tiering and motility. *Epifaunal motile* (facultative swimmers) include SUSP, Epi, Fat and SUSP, Epi, Funat; *Epifaunal recliner* include SUSP, Semi, Sunat and SUSP, Epi, Sunat; *Shallow infaunal* include DET, Is, Mf and SUSP, Is, Ms and SUSP, Is, Mf; *Endobyssate* include SUSP, Semi, Sat and SUSP, Is, Fat.

Ecological strategy	Prop. lower + prop. 0	Prop. higher + prop. 0
A		
DET, Is, Mf	0.5995	0.6564
SUSP, Epi, Fat	0.2071	0.9602
SUSP, Epi, Funat	0.3118	0.9335
SUSP, Epi, Sat	0.5830	0.5752
SUSP, Is, Ms	0.3159	0.8617
SUSP, Is, Mf	0.9989	**0.0059**
SUSP, Semi, Sunat	1	**0.0107**
SUSP, Semi, Sat	0.1309	0.9587
SUSP, Ip, Ms	0.0326	0.996
SUSP, Epi, Sunat	0.4556	0.8857
SUSP, Is, Fat	0.9758	0.1906
unknown	1	0.1622
B		
Epifaunal motile	0.0664	0.9872
Epifaunal recliner	0.9908	0.0414
Epifaunal attached	0.6044	0.5566
Shallow infaunal	0.917	0.1587
Deep Infaunal	**0.0236**	0.9974
Endobyssate	0.2382	0.8866
unknown	1	0

performed on the epifaunal bivalves only, as proposed by many authors (Hautmann, 2006; Kiessling et al., 2007; Hautmann et al., 2008a, 2008b). The results indicate that aragonitic epifaunal bivalves were more affected by the extinction than the bimineralic ones although the Chi-square test is not significant ($\chi^2 = 2.6902$, $p = 0.10097$) (Fig. 12B).

5. Discussion

5.1. Early and Middle Triassic bivalves: Paleozoic taxonomic and ecologic affinities

Early Triassic bivalve faunas were not very different (autoecologically) from those of the Permian, > and could be regarded as a much
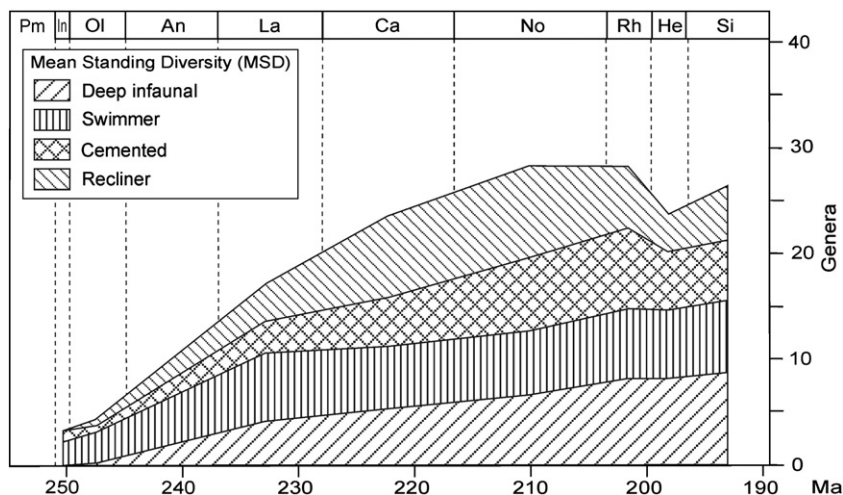

Fig. 10. Generic diversity (MSD) trends for four composite life strategy categories during the Induan–Sinemurian. Reclined bivalves are all suspensivorous, sedentary (non-motile), and unattached, and include epifaunal and semi-infaunal taxa. Swimming bivalves are all suspensivorous and epifaunal, and include facultative attached and facultative unattached taxas. Cemented bivalves are all suspensivorous, epifaunal, sedentary (non-motile), and attached. Deep burrower bivalves are all suspensivorous, deep infaunal, slow motile taxa.
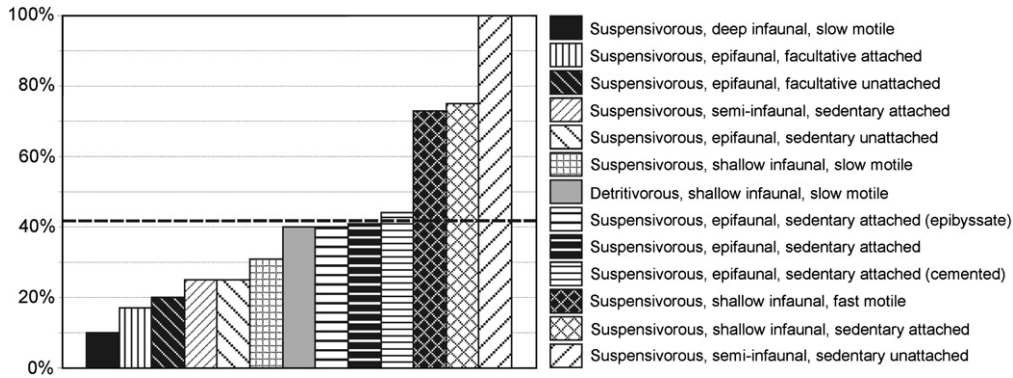
Fig. 11. Generic extinction rate by life strategy for the T/J crisis. The only significant differences from the global percentage extinction are observed for the Susp Semi Sunat and Susp Ip Ms strategies. *Broken line*: extinction for all categories combined (42%).

impoverished version of them. Most bivalve genera were survivors from the Permian and they were mainly epifaunal and semi-infaunal endobyssate taxa (see Appendix A). The earliest Triassic bivalve fauna was essentially cosmopolitan (Stanley, 1977a) and dominated, in terms of abundance, by *Eumorphotis*, *Promyalina* and *Unionites* (Fraiser and Bottjer, 2007). *Claraia*, although not as abundant (Fraiser and Bottjer, 2007), had a great specific richness (more than 30 species according to He et al., 2007, p. 1018). *Eumorphotis* and *Promyalina* did not reach the Middle Triassic, and the same occurred for 11 of the 23 survivors of the Permian. During the Middle Triassic, a great diversification is observed, and the main difference with Early Triassic was the beginning of diversification of cemented, deep burrowers and epifaunal motile bivalves, which were more important during the Late Triassic. The epifaunal attached (epibyssate) ecologic strategy included the most diverse fauna. Moreover, this strategy was the dominant one, in terms of abundance, among Middle Triassic bivalves (Bonuso and Bottjer, 2008).

5.2. Late Triassic–Early Jurassic bivalves and the MMR

During the Late Triassic some changes became apparent, both in the number of genera adopting certain strategies and in new adaptations probably linked to the increasing predator diversification as a result of the Mesozoic Marine Revolution. Although Vermeij (1977, 1983, 1987) located the beginning of the MMR in the Jurassic, it was later suggested that it may have already originated in the Triassic (Nützel, 2002; Hautmann, 2004b; Nützel and Erwin, 2004; Harper, 2005; Bonuso and Bottjer, 2008; Vermeij, 2008; Baumiller et al., 2010).

Infaunal bivalves increased in diversity and abundance throughout the Triassic, more noticeably from Late Triassic onwards (McRoberts, 2001; Bonuso and Bottjer, 2008) (Fig. 3A). At the same time, cemented bivalves diversified during Middle and Late Triassic (Harper, 1991) (Fig. 9B). Both infaunalization (Stanley, 1977a; Vermeij, 1977) and cementation (Harper, 1991, 2003; Hautmann, 2004b; Hautmann and Golej, 2004; Harper, 2005) were part of the response of bivalves to

the MMR, which reflects an increase in durophagous organisms. Harper (1991) verified experimentally that some predators (asteroids and crabs) prefer byssate rather than cemented bivalves (although cementation is not a protection against driller predators (Harper and Skelton, 1993)). During the Late Triassic (from Carnian to Rhaetian) there was a decrease in epibyssate bivalve diversity and an increase in cemented bivalve diversity (Fig. 9B), and at the same time the abundance of cemented bivalves rose (Bonuso and Bottjer, 2008). Post-Paleozoic cemented bivalves had more complex hinge plates than late Paleozoic ones, with massive hinge teeth (Hautmann and Golej, 2004), and new modifications of the alivincular ligament appeared polyphyletically in several groups (arcuate type in Ostreaidae and fossate type in Dimyidae, Plicatulidae and Spondylidae), which increased the stability of the valves' articulation (Hautmann, 2004b). These morphologic changes were interpreted by the last author as a defensive strategy against valve torsion and predator manipulation, and a resistance to valve opening.

Among epifaunal bivalves, motility also increased during the Triassic and Early Jurassic. Bivalves morphologically compatible with occasional swimming capabilities became more diversified (Ros, 2009), and at the Late Triassic a modification of the alivincular ligament appeared within the Pectinidae (alate type) in the genus *Indopecten* (Hautmann, 2004b). This ligament type enhances the power and effectiveness of the opening and closing movements of the valves, which permitted efficient swimming as an escape strategy (Hautmann, 2004b).

The post-Paleozoic success of both ostreoids and pectinoids was probably related to these new life habits, and associated also to the spreading of the foliated shell microstructure since the Triassic. This microstructure, though weaker than other types (such as nacre), has several other advantages, as the lower density for swimming and the capacity of building thick shells for cemented bivalves, together with a low metabolic cost because its organic content is low, and the potential for building various ornamentation types (Esteban-Delgado et al., 2008).

Reclined, epifaunal and semi-infaunal bivalves increased in diversity during the Triassic (Figs. 9A, F, 10; see also Harper, 2003, 2005), but from Norian on, they were less diverse, and they were strongly affected by the T/J crisis. This group was represented mainly by megalodontoids with very thick and large shells interpreted as a defensive trait (Vermeij, 1983, 1987; Harper and Skelton, 1993). Note that whereas cementing, swimming, and deep burrower bivalves increased in diversity throughout the Triassic, the reverse trend is observed for sedentary reclined bivalves during the Late Triassic and Early Jurassic (Fig. 10). During the Jurassic the same trend is observed with an increase in motility and infaunality and a decrease in the reclined mode of life (Aberhan et al., 2006).

Stanley (1977a) noted that endobyssate bivalves decreased in specific diversity during the Paleozoic probably due to increased diversity of predators, and this trend continued through the Triassic at
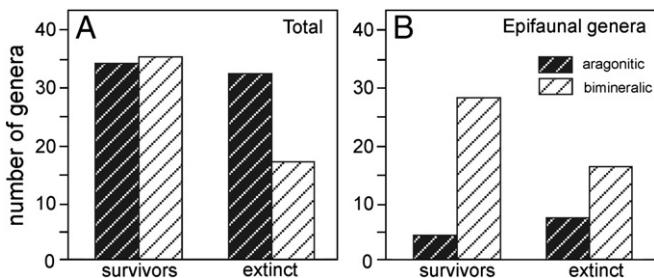

Fig. 12. Comparison of genera 1252 going extinct or surviving the T/J boundary crisis according to mineralogy. A. Total number of genera. B. Epifaunal genera.

genus level (28% at the beginning and 14% at the end of the stage) (Fig. 13).

Rock-boring bivalves re-appeared at the Norian with the genus *Lithophaga* (Kleemann, 1994) and perhaps also *Inoperna* at the Rhaetian (Hodges, 2000), although most authors interpreted this last genus as endobyssate semi-infaunal (Fürsich et al., 1995, 2001; Hautmann, 2001; Gahr, 2002; Delvene, 2003) based on the record of *Inoperna* in a semi-infaunal life position (Pojeta and Palmer, 1976). Stanley (1977a) suggested that the adoption of this mode of life was triggered by the increasing predation pressure. The borehole excavated by borer bivalves is an environment safe from most predators (Vermeij, 1987), similarly to the deep infaunal habitat (Stanley, 1977a). Deep infaunal bivalves increased in diversity during all Triassic, particularly from Late Triassic onwards (Fig. 9E) and there is a change in umbones position and pedal gape, and an increase of foot size, which allowed a greater burrowing efficiency (Runnegar, 1974).

Among shallow burrowers, Triassic Trigonioidea developed ornamentation which helps during burrowing (Stanley, 1977b), and Triassic and later Crassatelloidea and Carditioidea exhibit radial ornamentation and crenulated margins (Morris, 1978).

Though some authors argue that during the Triassic predators were not yet sufficiently abundant to influence bivalves (McRoberts, 2001), several predator groups experienced a rapid recovery after the P/T extinction, and already during the Middle Triassic their diversity had considerably increased (Walker and Brett, 2002). During the Late Triassic many of them experienced diversification (Table 3) and some of them (such as neoselachian and hybodontid sharks) had a considerably increase in abundance at least locally (Cuny et al., 2001). Even though there is no direct evidence of the activity of shell crushing predators, many of them already had the necessary adaptations for this predation method on molluscs in general and bivalves in particular (see Table 3). Direct evidences of shell crushing are recorded in the Middle Jurassic: probably predator fish regurgitation remains include abundant bivalves (*Trigonia*, *Myophoria*, *Gryphaea*, and others) (Zatón and Salamon, 2008). On the other hand, no drilling predators can be recognized as such, but shells with drilling holes made when the bivalves were alive are known from Late Triassic and Early Jurassic deposits (probably by gastropods, see references in Table 3). Asteroids already had the necessary adaptations to prey on bivalves as they do today during the Triassic (Donovan and Gale, 1990) and the same can be said about decapod crustaceans (Schweitzer and Feldmann, 2010).

The abundance of some of these predators (especially vertebrates) is probably underestimated by taphonomic factors and their fossil record cannot be used as evidence of the predation pressure (Harper, 2005). Moreover, predation marks may be difficult to detect in prey faunas, and Harper et al. (1998) suggested that predation levels can

be further underestimated. Because of the generally poor (often molds) preservation of early Mesozoic bivalves (Ros and De Renzi, 2005), it is indeed possible that Triassic predation levels have been underestimated, and that increased predation may be responsible for some of the life habit changes documented for this period (Harper et al., 1998; Harper, 2003). Probably because of their entirely calcitic shells, articulate brachiopod valves usually preserve predation marks better than bivalves (Harper, 2003). Perhaps not surprisingly, therefore, predatory drilling has been judged to be higher for brachiopods than for bivalves during the Mesozoic (Harper, 2003). Some brachiopods, such as terebratulids and rhynchonellids, already show a trend of ornamentation reinforcement during the Triassic and Jurassic. This trend was interpreted as a response to increased predator diversity (Vörös, 2010). Donovan and Gale (1990) even suggested that asteroid radiation could inhibit brachiopod re-radiation during the early Mesozoic.

Furthermore, influence of MMR during the Late Triassic can be seen in other organisms. Gastropods developed (independently in several phylogenetic lineages) high spired shells and strong reticulate knobby external ornament, features which were related to defense against predation and which were unknown in Paleozoic (Nützel, 2002; Nützel and Erwin, 2004). Crinoids experienced an important radiation during the Middle and Late Triassic, with an increment in the mobile forms, a trait directly related to predation by echinoderms (Baumiller et al., 2010). During the Late Triassic red calcareous algae developed adaptations to protect their tissues from herbivorous organisms (urchins and limpets), coraline algae with these new features radiated whilst solenopores (which did not develop them) decrease in diversity and eventually became extinct (Vamosi, 2005).

Late Triassic bivalve infaunalization was interpreted by McRoberts (2001) to result from greater competition in the epifauna than in the infauna, and from the biotic structure during the recovery phase after the P/T extinction. It is clear that siphonate bivalves (Stanley, 1968, 1977a), with access to many available niches without direct competition with other infaunal organisms during the Early Triassic (Bottjer et al., 2001), had a superb opportunity to radiate, and that their radiation was probably favored by the presence of post-Paleozoic predators that explain the other trends and adaptations which appeared at that time.

5.3. The Triassic/Jurassic extinction and recovery

Bivalve generic diversity rate increased continuously during the Triassic until the Norian, later it diminished, perhaps due to niche saturation. Bivalve origination rates show the highest peak during the Anisian and a lower one during the Carnian. Bivalve extinction rates show a different pattern than those suggested for the global biota by Lucas and Tanner (2008), where extinction rate decreased and origination rate increased continuously during the Upper Triassic. Bivalves show a high extinction rate during the Lower Triassic, the Carnian, and especially the Rhaetian (Fig. 5), but not during the Norian (at least at genus level), despite the fact that some groups, such as halobiids and monotiids suffered extinction at the Norian/Rhaetian boundary (McRoberts, 2007), and pectinids did so as well at the Carnian/Norian boundary (Johnson and Simms, 1989).The Trigoniida and Hippuritida show a maximum extinction rate during the Carnian (Ros and Echevarría, 2011), and their diversity then diminished during the entire Late Triassic. Nevertheless, the generic diversification rate is negative for bivalves only around the T/J boundary (Fig. 5). Bambach et al. (2004) noticed that the T/J global crisis was not characterized by extremely high extinction rates (as happened during the P/T crisis), but by moderate extinction rates combined with very low origination rates. This view was challenged by Alroy (2008) on the basis new data [Paleobiological Database], who identified the T/J crisis as a true mass extinction and this is the case of bivalves, since their extinction rate is high (compared with the rest of the Triassic) and their origination rate is only slightly low (Ros and Echevarría, in press). However, detailed regional studies (such as Mander et al., 2008 in SW England and south Wales) did not find evidence of
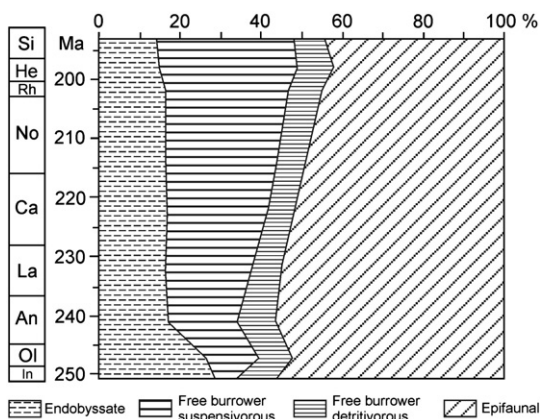

Fig. 13. Changes in the life habit groups during the Triassic and Early Jurassic (Hettangian and Sinemurian). Different plots show the mean percentage of genera in each life habit group for diversity of each stage.

Table 3

Suspected Triassic and Early Jurassic durophagous which predated on bivalves. Direct evidences only observed in shell-drilling predation. Shell-crushing and whole animal ingestion inferred by predator functional morphology. All groups originated or diversified during Triassic.

Predator		Type of predation	Evidences	Source	Origin or diversification
Sharks	Neoselachian sharks	Shell-crushing	Pointed teeth in front and flattened crushing teeth further back; specialized dentition, of crushing type	Carter, 1968; Cuny and Benton, 1999; Cuny et al., 2001	Triassic (present); Upper Triassic (radiation)
	Hybodontid sharks	Shell-crushing	Varied dentition, ranging from high-cusped impaling teeth to low-crowned crushers	Vermeij, 1987; Tintori, 1998; Cuny et al., 2001; Walker and Brett, 2002	Triassic (radiation); Upper Triassic (great diversification)
Fish	Pycnodontiform fish	Shell-crushing	Rounded, shell-crushing teeth, plus specialized nipping teeth; anterior, prehensil teeth are chisel-like in all known Triassic genera	Vermeij, 1987; Tintori, 1998; Lombardo and Tintori, 2005	Upper Triassic
	Semionotiform fish	Shell-crushing	Similar durophagus dentition; pointed antero-lateral teeth	Vermeij, 1987; Tintori, 1998; Lombardo and Tintori, 2005	Upper Triassic
	Macrosemiid fish	Shell-crushing	Crushing teeth in the median region of the lower jaw	Tintori, 1998	Upper Triassic
Placodonts		Shell-crushing	Large crushing tooth plates and procumbent premaxillary teeth	Carter, 1968; Vermeij, 1987; Walker and Brett, 2002; Benton, 2005	Middle Triassic
Ichthyosaurs (Omphalosauridae)		Shell-crushing	Heterodont dentition with large rear teeth	Walker and Brett, 2002; Montani, 2005	Middle Triassic
Rhynchosaurs		Shell-crushing	Specialized crushing beak and jaws	Carter, 1968	Triassic
Nautiloidea		Shell-crushing	Calcified jaws and direct evidences of crushing capacity	Vermeij, 1987; Kelley and Hansen, 2001	Triassic–Lower Jurassic
Crustaceans	Clawed homridian lobsters	Shell-crushing; whole animal ingestion	Heterochelous first pereiopods (molariform teeth appear in Lower Jurassic)	Vermeij, 1987; Schweitzer and Feldmann, 2010	Lower Triassic
	Spiny lobsters (Palinuroidea)	Shell-crushing	Robust mandibles	Vermeij, 1987; Walker and Brett, 2002; Schweitzer and Feldmann, 2010	Upper Triassic (Norian)
Unkown gastropods		Shell-drilling	Predation scars (boreholes)	Fürsich and Wendt, 1977; Végh Neubrandt, 1982; Newton, 1983; Fürsich and Jablonski, 1984; Newton et al., 1987; Harper et al., 1998; Kowalewski et al., 1998; McRoberts and Blodgett, 2000; Harper, 2003, 2005	Upper Triassic + Lower Jurassic
Asteroidea		Whole animal ingestion; insertion and extraction	Morphology similar to living predatory Asteriidae (?): muscular arms and sucking tube feet, flexible mouth frame and eversible stomach	Carter, 1968; Vermeij, 1977; Donovan and Gale, 1990; Harper, 1991; Blake and Hagdorn, 2003; Harper, 2005	Middle Triassic (present), Jurassic (diversification)

cathastrophic extinction in taxonomic terms but, instead, show evidence of palaeoecological change in the benthic marine ecosystem around the T/J boundary.

The intensity of the T/J crisis may have been overestimated due to the "compiled correlation effect" of imprecise stratigraphic data, the Signor–Lipps effect (Signor and Lipps, 1982), and extrapolation of local data to a global scale (Lucas and Tanner, 2008). The real magnitude of this T/J extinction event is difficult to evaluate due to the widespread facies changes which characterize the T/J boundary (Jablonski, 2005), with the disruption of calcareous sedimentation by dominant siliciclastic deposits which do not favor the preservation of calcareous skeletons (Hautmann, 2004a).

5.3.1. Extinction selectivity

The present study does not support previous conclusions that infaunal bivalves suffered greater extinction than epifaunal ones during the T/J extinction (McRoberts and Newton, 1995; McRoberts et al., 1995, in Europe; Hautmann et al., 2008b, in Tibet; Kiessling et al., 2007, for whole bivalve biota) (Fig. 5). The extinction rate was similar for both collectives as noted by McRoberts (2001), although origination rate was higher for infaunal ones and therefore the diversification rate was higher for this collective. The data also indicate that during the Carnian, Norian, and the post-Triassic recovery phase, extinction rate was lower whilst origination rate was higher for infaunal bivalves (Fig. 5; see also Kiessling et al., 2007). Although some regional studies (mentioned above for Europe and Tibet) based on species level-data and resolved at sub-stage time intervals reveal certain patterns and events that cannot be observed at higher taxonomic ranks, we have to take into account that infaunal bivalves (mostly aragonitic) were under-represented

during Mesozoic molluscan-dominated communities and probably the diversity estimates are biased in this sense (Wright et al., 2003).

The positive selection of deep burrowers (mainly pholadomyoids) can be explained in terms of the "safe" habitat they occupied. Deep infaunal habitat could be a refuge and an isolated environment which protected the organisms from unpredictable environmental perturbations. Diverse environmental stress factors, such as wave energy, salinity, oxygen deficiency, temperature, competition for space and resources, predation, etc., can differentially affect bivalves and other organisms in marine habitats (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). Kauffman (1978) observed that Cretaceous deep burrower species had higher longevities and lower evolutionary rates than species which occupied higher places in the infauna. This was fostered by these stress gradients and was probably also the case in T/J extinction.

Semi-infaunal reclined bivalves were all megalodontoids. It was suggested that megalodontoids (Superfamily Megalodontidae) could establish photosymbiotic relationships with microorganisms (Freitas et al., 1993; Yancey and Stanley, 1999; McRoberts, 2001), similarly to other bivalve groups, such as Cretaceous rudists (Kauffman and Johnson, 1988) or Permian Alatoconchidae (Isozaki, 2006). Nevertheless, megalodontoid morphology could be just an adaptation to a reclined mode of life. Several authors (e.g., Vogel, 1975; Seilacher, 1990; Jones and Jacobs, 1992) established some criteria to recognize photosymbiosis in fossils when other interpretations are ruled out. Some of them agree with megalodontoid morphology (great size, thick shells, inhabiting shallow waters in tropical environments, aberrant morphology). But many living species with photosymbionts do

not have special shell features, and, conversely, some species which do have these traits do not bear photosymbionts (Jones and Jacobs, 1992; Savazzi, 2001). Megalodontoids are frequently associated to carbonaceous facies and are almost always associated to tropical warm water shallow environments (Végh Neubrandt, 1982). Their shells are heavy and thick, and particularly during the Norian and Rhaetian they reached large sizes (up to 42 cm, Végh Neubrandt, 1982, p. 45; 50–60 cm, Allasinaz, 1992, p. 447). Several members of this superfamily had aberrant morphologies (e. g. *Dicerocardium* or *Wallowaconcha*) which can be associated to photosymbiosis (see Seilacher, 1990). Together with megalodontoid size increase, there was an increase in scleractinian coral reefs (Payne and Van de Schootbrugge, 2007). In their benthonic life analysis Kiessling and Aberhan (2007, p. 428) conclude that tropical organisms are much more affected than others, and bivalve data agree with this, though bivalves with tropical affinities were few. These authors explain this selectivity by the climatic changes related to the T/J extinction.

Regarding fast shallow burrowers, the most affected were the Trigoniida (Ros and Echevarría, 2011). They were the most strongly ornamented shallow burrower bivalves during the Rhaetian. This ornamentation was interpreted as aiding in burrowing (Stanley, 1977b) but can also be related to shell reinforcement and as a defensive response to predators which appeared and diversified during post-Paleozoic times (e.g. Vermeij, 1983). The most escalated (heavily armored) prey taxa, with greater energetic requirements, were the most affected by environmental deterioration, a trait related to mass extinction, i. e., the mass extinctions interrupts the escalation (Vermeij, 1987). Triassic times were the beginning of Mesozoic marine revolution and the T/J extinction could disrupt the beginning of escalation. The causes of this negative selection are related with the Central Atlantic Magmatic Province and discussed in a work in progress (Ros and Echevarría, in preparation).

Regarding shell mineralogy, Hautmann (2004a, 2006) and Hautmann et al. (2008a) suggested that ocean acidification at the T/J boundary could cause wholly aragonitic bivalves to suffer greater extinction than bimineralic ones. In this context, it is significant that shell mineralogy and mode of life are highly correlated (De Renzi and Ros, 2002), with burrowing bivalves being nearly exclusively aragonitic. The present study confirms that during the T/J crisis (Fig. 12A), wholly aragonitic bivalves suffered proportionally more extinction than bimineralic ones although non-statistically significant differences are detected in the results. However, this could be related to their predominantly shallow infaunal motile mode of life rather than to their shell mineralogy. According to Kiessling et al. (2007, p. 216) aragonitic epifaunal bivalves were more vulnerable to extinction during the Triassic and Jurassic than bimineralic epifaunal bivalves. However, our data (Fig. 12B) demonstrate that most of the epifaunal bivalves which became extinct were bimineralic and the extinct epifaunal aragonitic genera were almost all recliners (epifaunal and semi-infaunal non motile unattached).

5.3.2. Taxonomic versus ecologic changes

Hallam (1981) proposed a more severe generic-level T/J extinction for bivalves (50%) than the 42% extinction indicated by our data. Our percentage is more similar to that in McRoberts (2001; 40%), and higher than that in Hallam (2002; 31%), Kiessling et al. (2007; 26 ± 5%), and Hautmann (2007, 34%). Our generic data do not reflect the global Norian–Rhaetian extinction event described by Lucas and Tanner (2008) for bivalves and other organisms. Instead, we see a mild extinction rate during the Carnian and Anisian, a much higher rate during the Rhaetian, but no extinction peak during the Norian.

Despite the loss of 42% of genera, bivalves were unaffected in terms of life habit strategies at the T/J boundary. The taxonomic and ecologic impact of the extinction was therefore decoupled, as previously noted by Droser et al. (2000) and McGhee et al. (2004) for

other extinction events for the whole biota. Droser et al. (1997) developed a system to evaluate the severity of ecologic change produced during mass extinctions and recoveries. They considered four paleoecologic levels, all non additive and non hierarchical, but ordered by severity. They also indicated some characteristic signals for each level. We have modified these levels and their signals to better evaluate the ecologic severity of extinction in the Bivalvia (Table 4). We conclude that the T/J boundary shows no change in the ecology of bivalve communities, no loss of any bivalve life strategy, and only third and fourth level ecologic changes, indicated by "thinning" within life strategies and taxonomic changes. In contrast, the P/T extinction was characterized by second level ecologic changes for bivalves, with the transition from brachiopod- to bivalve-dominated shelf communities during the Early Triassic (Gould and Calloway, 1980). The T/J extinction did not even see a change in infaunal tiering, with deep burrowers losing only one genus.

5.3.3. Post P/T and post T/J recoveries

A comparison of bivalve diversity at the beginning of the Triassic and Jurassic indicates that the two post-extinction recoveries were quite different. The Early Triassic was characterized by several generalized bivalves with wide paleogeographic distributions, whereas the Early Jurassic was characterized by much greater bivalve diversity. One shared feature was the small size of the recovery bivalves (Twitchett, 2001), as clearly shown by megalodontids at the T/J boundary (Végh Neubrandt, 1982; Hautmann, 2006) and by other bivalves at the P/T boundary (Hautmann and Nützel, 2005). Although ecologic tiering is usually affected during extinction events (and that indeed happened during the P/T crisis), no such changes are evident for bivalves at the T/J boundary.

During the Hettangian and Sinemurian (Early Jurassic), the rapid recovery of infaunal bivalves correlates with the Jurassic infaunalization described by Aberhan et al. (2006).

The number of new genera appearing during the Hettangian (21) is nearly the same as those appearing during the Early Triassic (20), but the time involved is much shorter, i.e., 3.1 Myr for the Hettangian and 6 Myr for the Induan + Olenekian. The faster rate of recovery during the Early Jurassic reflects the smaller magnitude of the T/J crisis compared with the P/T crisis, and probably also the greater ecologic impact of the P/T event.

6. Conclusions

Triassic was first a recovery period and later a biotic diversification time for bivalves. During the study interval, generic diversity climaxed during the Norian, but later it diminished, probably due to niche saturation. Bivalve origination rates were highest during the Anisian. Generic diversification rates were negative for bivalves only around the T/J boundary. Bivalves show a high extinction rate during the Lower Triassic, the Carnian, and especially the Rhaetian, but not during the Norian, despite the fact that some groups, such as halobiids and monotiids, suffered extinction at the Norian/Rhaetian boundary.

Table 4
Paleoecologic levels and their typical signals to evaluate the effects of extinctions and recoveries among bivalves. (Modified from Droser et al., 2000).

Level	Signals
First	1—initial radiation of the clade
	2—total extinction of the clade
Second	1—changes in dominance with respect to other clades
	2—appearance/disappearance of bivalve ecospace strategies
Third	1—increase and/or decrease of tiering complexity
	2—"filling" or "thinning" within bivalve ecospace strategies
Fourth	1—taxonomic changes within the clade
	2—appearance/disappearance of the clade in certain communities

Early and Middle Triassic faunas were autoecologically similar to Permian ones. During the Middle Triassic, cemented, deep burrowers and epifaunal motile bivalves began to diversify, and were more important during the Late Triassic. The process of infaunalization was suddenly improved for bivalves in the Late Triassic, and proceeded unabated throughout the Mesozoic. This development, and the selectivity against free-lying forms during the same period of time, together with a diversity increase in cemented and facultative motile bivalves, seems to reflect the influence of the MMR. However, possibly due to the generally poor preservation of early Mesozoic bivalve faunas, the link between these changes and increased predation in the Triassic can be only inferred by indirect evidences and has yet to be demonstrated by direct evidences.

The cohort analysis shows that among genera with Induan to Sinemurian FADs, the survivorship of infaunal bivalves was greater than the epifaunal collective mainly for Lower Jurassic genera. The greatest longevities are observed in genera which originated after P/T crisis, during Early Triassic, and, after T/J crisis, during Hettangian. The lowest longevities are those of genera originated during the Carnian, the Triassic stage with major diversification and turnover.

The statistical significance of T/J extinction selectivity was tested, and shows a positive selection of deep burrowers, contrary to previous conclusions that infaunal bivalves suffered greater extinction than epifaunal ones. The data also indicate that during the Carnian, Norian, and the post-Triassic recovery phase, extinction rate was lower whilst origination rate was higher for infaunal bivalves. Regarding fast shallow burrowers, the most affected were the Trigoniida.

The present analysis indicates that taxonomic and ecologic impact of the Triassic–Jurassic extinction was decoupled: although the crisis strongly impacted bivalve taxonomic diversity (a loss of 42% of genera), it had little impact on bivalve ecologic diversity. Not a single bivalve life strategy was eliminated at the end of the Triassic and infaunal tiering was unaffected, with only third and fourth level ecologic changes. In contrast, the P/T extinction was characterized by second level ecologic changes for bivalves, with the transition from brachiopod dominated to bivalve dominated shelf communities during the Early Triassic.

Acknowledgments

Appendix A

Induan–Sinemurian marine bivalve genera arranged by ecologic strategy. Bold: origination; underlined: extinction; bold and underlined: origination and extinction in the same stage. Ecologic strategies: Susp: suspensivorous; Det: detritivorous; Epi: epifaunal; Semi: semi-infaunal; Is: shallow infaunal; Ip: deep infaunal; Mf: fast motile; Ms: slow motile; Fat: facultative attached; Funat: facultative unattached; Sat: sedentary (non motile) attached; Sunat: sedentary (non motile) unattached. (C): cemented, (B): borer.

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