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The impact of the Pliensbachian–Toarcian crisis on belemnite assemblages and size distribution

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Abstract

The second-order Pliensbachian–Toarcian crisis affected major groups of marine organisms. While its impact has been intensively studied for ammonites, the response of belemnites is only currently emerging through quantitative studies. Novel overall and regional diversity analyses suggest that belemnite richness in the NW-Tethys drops at the Pliensbachian–Toarcian boundary, while overall diversity slightly increases in NW-Tethys assemblages during the Toarcian Oceanic Anoxic event (T-OAE), mostly driven by NW European assemblages (e.g., Yorkshire). The T-OAE coincides with marked taxonomic turnover within individual basins, which is associated with an increase in median rostrum size of specimens in taxa at most localities. The changes in median body size across the Pliensbachian–Toarcian boundary are less consistent and driven by changes in body size within individual lineages crossing the boundary. However, our analyses also illustrate differences in sampling across the Pliensbachian–Toarcian crisis, which needs to be considered in further studies.

Keywords: Cephalopoda, Belemnitida, Rarefaction, Rostrum size, Paleoecology, Sampling

Introduction

After their appearance in the Late Triassic (Iba et al., 2012), belemnite cephalopods become important pelagic components of Jurassic–Cretaceous ecosystems (Hoffmann & Stevens, 2020). The Early Jurassic radiation of this group, which is now considered the stem-group of modern decabrachians (Fuchs et al., 2016; Hoffmann & Stevens, 2020), is interrupted by the Pliensbachian–Toarcian crisis (Dera et al., 2016). A recent analysis of available data confirmed a marked impact of the Pliensbachian–Toarcian crisis on their diversity (Neige et al., 2021), but it mostly relied on data from NW European localities. Various studies focusing on basins in the Euro-Boreal domain have suggested a marked impact of this crisis on the belemnite biogeography, diversity, and morphology (Caswell & Coe, 2014; Dera et al., 2016; Doyle, 1987; Morten & Twitchett, 2009; Rita et al., 2018). Most authors recognize that the crisis might encompass at least two major pulses of extinction (Caruthers et al., 2013; Cecca & Macchioni, 2004; Dera et al., 2010; Little & Benton, 1995), one at the Pliensbachian–Toarcian boundary event (PToB) and one during the Toarcian Oceanic Anoxic event (T-OAE). However, studies of belemnites are rarely resolved at the ammonoid zonal to subzonal level so that the effects of these events can barely be teased apart (Dera et al., 2016). Both pulses have been linked with climate-related stressors (CRS), itself likely triggered by volcanic activity in the Karoo-Ferrar province

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(Müller et al., 2020; Ruebsam & Al-Husseini, 2020; Ruebsam et al., 2020; Suan et al., 2010). Previous studies have also linked these pulses to changes in body size distribution with assemblages of various animal clades (Caswell & Coe, 2013; Caswell & Dawn, 2019; García Joral et al., 2018; Martindale & Aberhan, 2017; Morten & Twitchett, 2009; Piazza et al., 2019, 2020; Ros-Franch et al., 2019) including belemnites (Nätscher et al., 2021; Rita et al., 2018, 2019). The relative contribution of within-species fluctuations versus taxonomic turnover in driving such size fluctuations in assemblages still needs to be more widely understood (e.g., Twitchett, 2007; Rego et al., 2012). Reconstructing changes in belemnite diversity, biogeography and size distributions during this crisis is complicated by variations in sea-level and sedimentation rates, which also affected belemnite abundance and habitats (Morard et al., 2003; Pittet et al., 2014; Rita et al., 2018, 2019).

Research on belemnites from the Pliensbachian–Toarcian interval has often focused on their geochemical properties rather than on their evolutionary and paleobiological features (Gómez et al., 2008; Harazim et al., 2013; McArthur et al., 2000; Ullmann et al., 2014; van de Schootbrugge et al., 2005). Meanwhile, paleobiological research has often targeted their distant relatives, ammonoid cephalopods (Caruthers et al., 2013; Dera et al., 2010, 2011; Gerber, 2011; Guex et al., 2012). Over the last years, new belemnite research including also (sub) Mediterranean localities (Pinard et al., 2014; Rita et al., 2019, 2021; Sanders et al., 2015; Weis et al., 2018) allows us to tackle the paleobiological and evolutionary impact of the crisis on Pliensbachian–Toarcian belemnites more precisely.

We herein focus on 5 regions where both size data and belemnite relative abundance at the zonal level are available across the Pliensbachian–Toarcian boundary and/or the T-OAE (i.e., Asturian Basin = RODI, Cleveland Basin = YORK, Lusitanian Basin = BEIR, Eastern Paris Basin = LUXE, Western Paris Basin = NORM). Detailed size data are not available across the Pliensbachian–Toarcian for the Causses (CAUS), but diversity comparisons are made where possible. To place these patterns in a larger context, we also compare our results with changes in community composition across the NW-Tethys based on vetted species occurrences from a wider range of localities (Fig. 1) from the Margaritatus (Pliensbachian) to Variabilis chronozones (Toarcian) updated from Neige et al. (2021). Although the names of some zones differ among localities, we use the zonal names of the northwest European province (Dean et al. 1961, Elmi et al. 1994, 1997, Dommergues et al. 1997) for all equivalent zones in other provinces in this study for the sake of simplicity and understandability.

We test and compare how belemnite richness, species composition, and size distribution changed during the first pulse (transition from the Spinatum to Tenuicostatum Zone) and the second pulse of the Pliensbachian–Toarcian crisis (transition from the Tenuicostatum to Serpentinum Zone including the T-OAE).

Material and methods

Here, we updated the NW-Tethys dataset from Neige et al. (2021) with additional occurrence data from Normandy (NORM), Rodiles in the Asturian Basin (RODI) and Peniche in the Lusitanian Basin (BEIR) from the Spinatum to Serpentinum Zones based on new field and quantitative sampling. We extended the range of 3 species (*Parapassaloteuthis zieteni*, *Passaloteuthis laevigata* = *bisulcata*, *P. milleri*) into the Spinatum Zone for the Cleveland Basin (YORK) to be consistent with data compiled from Little (1995) and Doyle (1990, 1992) as summarized by Caswell and Coe (2014) and used by Rita et al. (2021). To allow for comparison, we used the same approach and abbreviations as Neige et al. (2021) with the updated version of the corresponding dataset (Appendix S2 of Neige et al., 2021) to evaluate richness patterns and sampling completeness (Fig. 1). Sample-based and coverage-based rarefaction and extrapolation were used to evaluate species richness for a standardized number of 16 localities and a sampling coverage of 75%. The online version of iNEXT (Chao et al., 2016) was used for the computation (number of knots set to 40 and 95% confidence intervals being generated after 1000 bootstraps). We further assessed the effects of updating the dataset of Neige et al. (2021) upon the mean values of the asymptotic richness estimators Chao 2 (Anne Chao, 1984, 1987) and ICE (Anne Chao & Lee, 1992; Chazdon et al., 1998). Computations were made with EstimateS 9.1.0 (Colwell, 2013) with the same settings as those described in Neige et al. (2021).

We also used this modified dataset to run a multivariate ordination analysis, namely non-metric multidimensional scaling (NMDS), for investigating assemblage changes across NW-Tethys using vegan in R (Oksanen et al., 2020). On the same dataset and package, we performed an analysis of similarity (ANOSIM, Clarke, 1993) to test if the differences in assemblage composition were significant between the Pliensbachian (Margaritatus and Spinatum zones), lowermost Toarcian (Tenuicostatum Zone) and the rest of the Toarcian (Serpentinum, Bifrons and Variabilis Zones). We also performed a similarity percentage analysis (SIMPER, Clarke, 1993) on this dataset to identify the species that contribute the most to dissimilarity across these units.

We focus our analyses on 5 basins (Asturian (RODI), Lusitanian (BEIR), Western and Eastern Paris (NORM

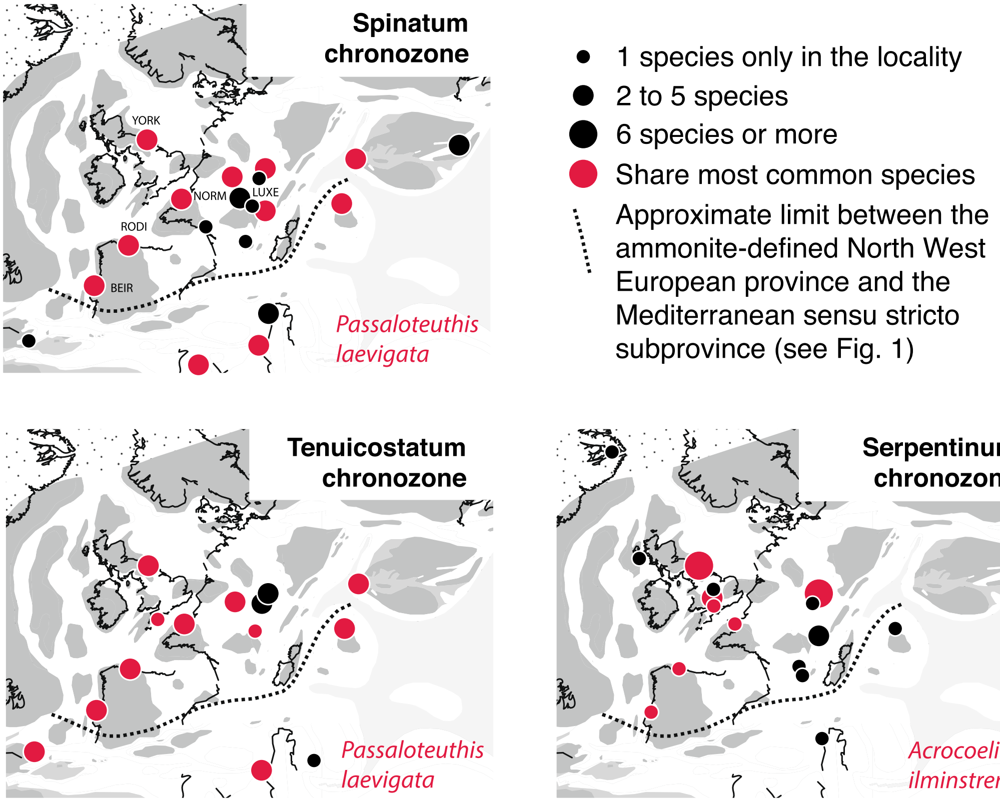


Fig. 1 Paleogeographical distribution of belemnite occurrences during the Spinatum, Tenuicostatum and Serpentinum Zones. The localities yielding the most reported species are marked in red (modified from Neige et al., 2021). Note that the Lusitanian basin is herein assigned to the edge of Euro-boreal realm (NW-European domain), but in some analyses it belongs to the Mediterranean realm (Mediterranean domain) during the early Toarcian (Dera et al., 2011)

and LUXE) and Cleveland (YORK) Basins) for which body size data, as well as relative abundance data are available for at least 3 consecutive zones. Note that for the Eastern Paris Basin (LUXE), size data for some zones are missing. Relative abundance are available for Lusitanian Basin (Peniche; Rita et al., 2021), Asturian Basin (Rodiles; Rita et al., 2021), Western Paris basin (Fresney-le-Puceux and Feuguerolles-sur-Orne; Weis et al., 2018 supplemented with abundance data from Rita et al., 2021), Cleveland Basin (as compiled from Caswell & Coe, 2014; Doyle, 1990, 1992; Little, 1995). The available belemnite data from the South Riffian Basin are restricted to the Serpentinum (Levisoni) Zone (Bardin et al., 2015; Sanders et al., 2015) and relative abundance and size data are currently too patchy for the Swabo-Franconian basin as sufficient data are not consistently reported at zonal level resolution (Riegraf et al., 1984; Schlegelmilch, 1998). However, these as well as all other localities in NW-Tethys used in Neige et al. (2021) were included in wider-scale analyses based on presence/absence data.

For individual regions in which abundance data are available, a bootstrapping method (Gotelli et al., 2010; Nätscher et al., 2021) was adapted to test for non-random changes in the species composition of the communities across zones. For each location, 500 communities ($n_{\text{individuals}} = $ mean sample size per zone) were simulated by repeatedly drawing from the species names found there. The likelihood of each species to be drawn is its relative abundance in the overall sample with all zones pooled. For each of the 500 simulated communities, the relative abundance of each species is calculated. Relative abundances of species in zones of the real sample, that fall between the minimum and maximum values of simulated relative abundances are within the range of random sampling differences.

For the regional rarefied richness, we mostly relied on previously published datasets (Rita et al., 2021) with the exception of the Eastern Paris Basin (LUXE). We calculated rarefied richness (at sample size $n = 20$) using the specimens which were at our disposal to do the size analyses for the latter. Although we have more highly resolved data on the ammonoid subzone or bed level for some localities (Asturian Basin, Lusitanian Basin), we consistently analyzed belemnite body size changes at the zonal level as such a resolution was available for the 5 basins we consider here.

Belemnite rostrum size data are available from previous published work (Rita et al., 2019) as well as unpublished data compiled in the framework of undergraduate and graduate theses (Asturias: Rita et al., 2019; Cleveland Basin: Peter Laschinger, 2019; Eastern and Western Paris Basin and Causses: Christof Übelacker, 2010).

To allow comparisons between differently shaped species and avoid taphonomic overprint as much as possible, we use the geometric mean (GM) of the apical length (l), height (Dv) and width (Dl) of the rostrum solidum of each specimen as a proxy for body size (Rita et al., 2018). This relates to the fact that preservation of soft-tissues is too rare and that parts of the rostrum cavum are often broken making it difficult to obtain the original total length (L) of rostrum (Klug et al., 2021; Nätscher et al., 2021; Reitner & Urlichs, 1983; Rita et al., 2018). We use all available GM of specimens from a particular region to calculate the median body size. In the case of the Eastern Paris Basin, where most data were only available for the length of rostrum solidum, changes in rostrum solidum where rescaled to GM using the positive correlation between GM and l. This should be acceptable as it was demonstrated that GM and l are consistent with each other and only slightly differ in magnitude (Rita et al., 2018). Size measurements of specimens in assemblages sampled from zones were decomposed in within-lineage (specimens belonging to species present in both bins) and between-lineage components related to the disappearance of species present in the first interval (effects of specimens belonging to species which go extinct or emigrate) or the appearance of species in the second interval (effect of specimens belong to species which appear or immigrate). This approach was first introduced by Rego et al. (2012) and modified by Rita et al. (2019). To visualize the size changes seen in the different components (assemblage, taxa appearing, taxa disappearing, within-lineage changes) on two axes, we performed a principal component analysis.

Results

Richness

When investigating individual regions, the raw richness shows slight decreases to status quo in diversity across the Pliensbachian–Toarcian boundary (Fig. 1; see also Additional file 1: Fig. S1). In the Western Paris Basin (NORM), there is an increase, due to the small sample size in belemnites in the Spinatum Zone. When focusing only on rarefied richness curves, there is a decrease in richness in all the localities that have sample size > 20 (Fig. 2A).

The changes around the T-OAE are more disparate, with three localities (BEIR, NORM, RODI) showing decreases in belemnite abundance and raw richness, while one NW European locality (YORK) show a clear increase in richness at the zonal level in raw richness. Detailed studies around the T-OAE are complicated by the low abundance of regional studies allowing rarefied richness analyses across this interval. Nevertheless, differences between localities remain also in our rarefied diversity analyses with one NW locality showing evidence for a diversity increase (Cleveland Basin: YORK) and another with evidence for a diversity decrease (Eastern Paris Basin: NORM) at the zonal level.

When redoing the global diversity analyses based on species present for all available localities in the NW-Tethys including new data from the sub-Mediterranean and NW European basins, the diversity drops from the Spinatum to the Tenuicostatum Zone and a slight increase in the Serpentinum Zone remains visible at the zonal level.

Compared to the results of Neige et al. (2021), (Fig. 2C), the updated curve (Fig. 2B) shows a slightly less steep decrease in the Spinatum–Tenuicostatum–Serpentinum interval, but it remains largely within the previous range of the 95% confidence intervals, suggesting that the update does not critically alter the pattern at that scale. The same is true for sampling coverage computed for 16 localities, with a slight increase for the Tenuicostatum Zone (see sampling coverage in the Additional file 3).

(See figure on next page.)

Fig. 2 **A** Regional belemnite species richness rarefied to 20 specimens where possible. Boxes refer to the relative availability of localities with a suitable sample size; **B** belemnite raw species richness (updated curve) compared to the corresponding estimators Chao 2 (light grey line) and ICE (grey dotted line); confidence intervals for raw richness are derived from the unconditional variance computed for sample-based rarefaction; for the Chao 2 estimator, only the lower bound of the 95% confidence interval is shown for clarity; **C** Belemnite species richness rarefied or extrapolated to 16 localities and associated 95% confidence intervals; data are plotted at the mid-points of the time scale of Gradstein et al. (2012). The lower part of the figure shows the chronostratigraphic framework used here (Ja, Jamesoni; Ib, Ibex; Da, Davoei; Ma, Margaritatus; Sp, Spinatum; Te, Tenuicostatum; Se, Serpentinum; Bi, Bifrons; Va, Variabilis; Th, Thouarsense; Di, Dispansum; Ps, Pseudoradiosa; Aa, Aalensis). Red arrows and dotted vertical red lines indicate the two pulses of the second-order Toarcian crisis

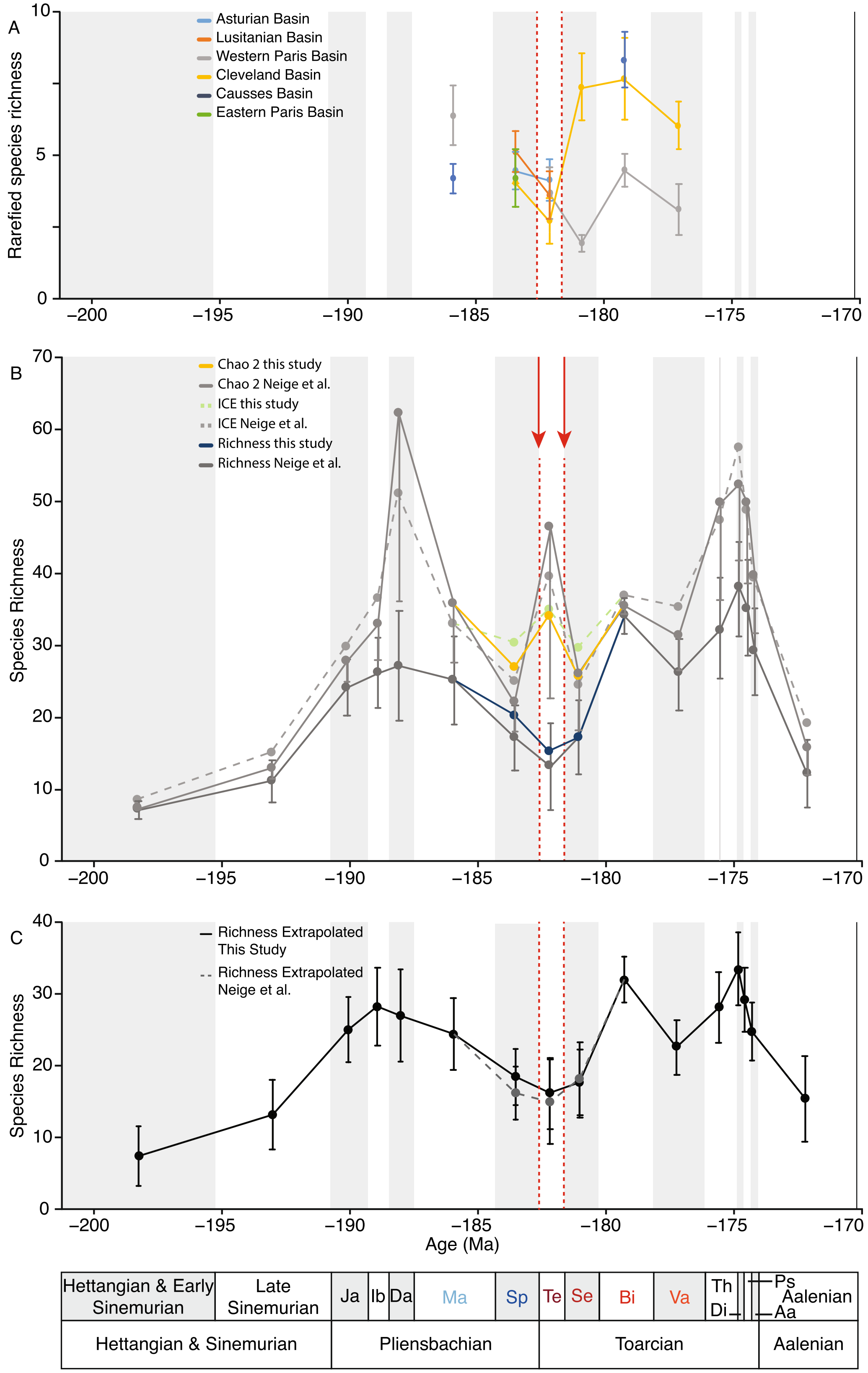


Fig. 2 (See legend on previous page.)

After updating the dataset of Neige et al. (2021), the mean values of the asymptotic richness estimators Chao 2 and ICE slightly decreased, especially in the Tenuicostatum Zone (Fig. 2B). This corroborates that the new data included here contributes to narrowing the gap between the observed and the expected belemnite richness. It also suggests that adding even more data will significantly contribute to a better understanding of this critical turnover interval in the macroevolutionary history of belemnites.

Species composition

When analyzing species composition using the updated occurrences, the assemblages during the Margaritatus, Spinatum and Tenuicostatum zones show strong compositional similarity (Additional file 2: Fig. S2). This is also visible in the NMDS (Fig. 3) and supported by the results of the ANOSIM analysis (Bonferroni-corrected *p*-values = 1) which could not reject the null hypothesis that there was no difference between these zones. The dominating species does not markedly change when going from Spinatum to Tenuicostatum Zone which has the lowest overall average dissimilarity (72,1) in the SIMPER analysis (Fig. 4). In both zones—*Passaloteuthis laevigata*, together with *Parapassaleuthis zieteni*, *Catateuthis longiformis*, *Passaloteuthis milleri*, are the most frequently shared species (Additional files 4, 5, 6, 7, 8, and 9).

There is, however, a marked shift when going from the Tenuicostatum to the Serpentinum Zone which coincides with the extinction of previously common species (*Passaloteuthis laevigata*, *Parapassaloteuthis zieteni* and *Catateuthis longiforma)* and marks the high frequency of *Acrocoelites ilminstrensis* and other species (*Acrocoelites trisulculosus*, *Cuspiteuthis tubularis*) within assemblages. This transition also yielded significant differences in the ANOSIM analysis (both at the zonal level with *p*-value = 0.0015 as well as when comparing pre-T-OAE with post-T-OAE zones with *p*-value = 0.0081). When analyzing the changes in belemnite occurrences in individual localities from the Tenuicostatum to Serpentinum Zones, as this is where most changes in species composition seem to occur, we found the largest overall average dissimilarities in the consecutive zonal comparisons with the SIMPER analysis (98,7; Fig. 4). The cumulative dissimilarities of species disappearing (*Passaloteuthis laevigata*, *Parapassaleuthis zieteni*, *Catateuthis longiforma*) and appearing (*Acrocoelites ilminstrensis*) explain almost 47% of the total dissimilarity. This is consistent with previous NMDS and ANOSIM analyses (Rita et al., 2021) showing the largest changes across the T-OAE focusing on the better sampled basins (Asturian, Causses, Cleveland, Lusitanian, South Riffian, Swabo-Franconian and Western Paris Basins).

This pattern is also seen in the bootstrapping approach (Fig. 5), which revealed that, while in all basins, changes

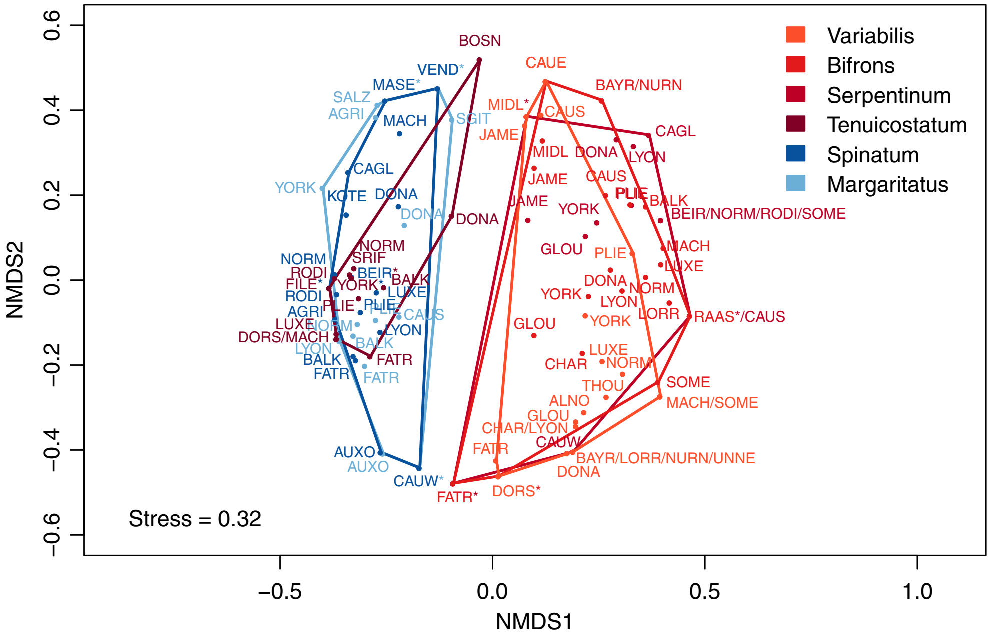


Fig. 3 NMDS analysis of species occurrences deriving from different basins and zones (dissimilarity metric = Bray Curtis). Stress Value = 0.32 (minimum stress value obtained after several runs)

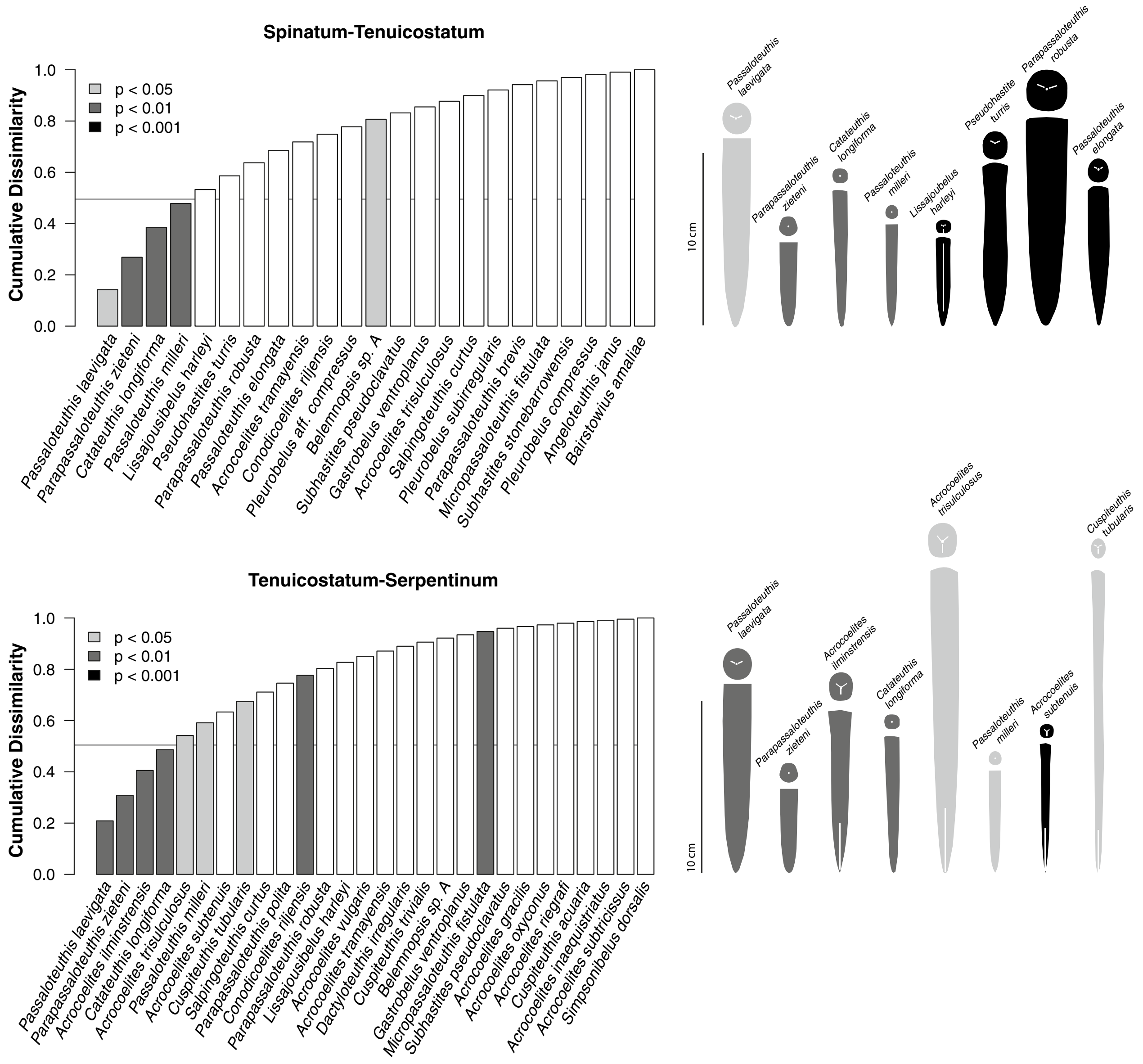
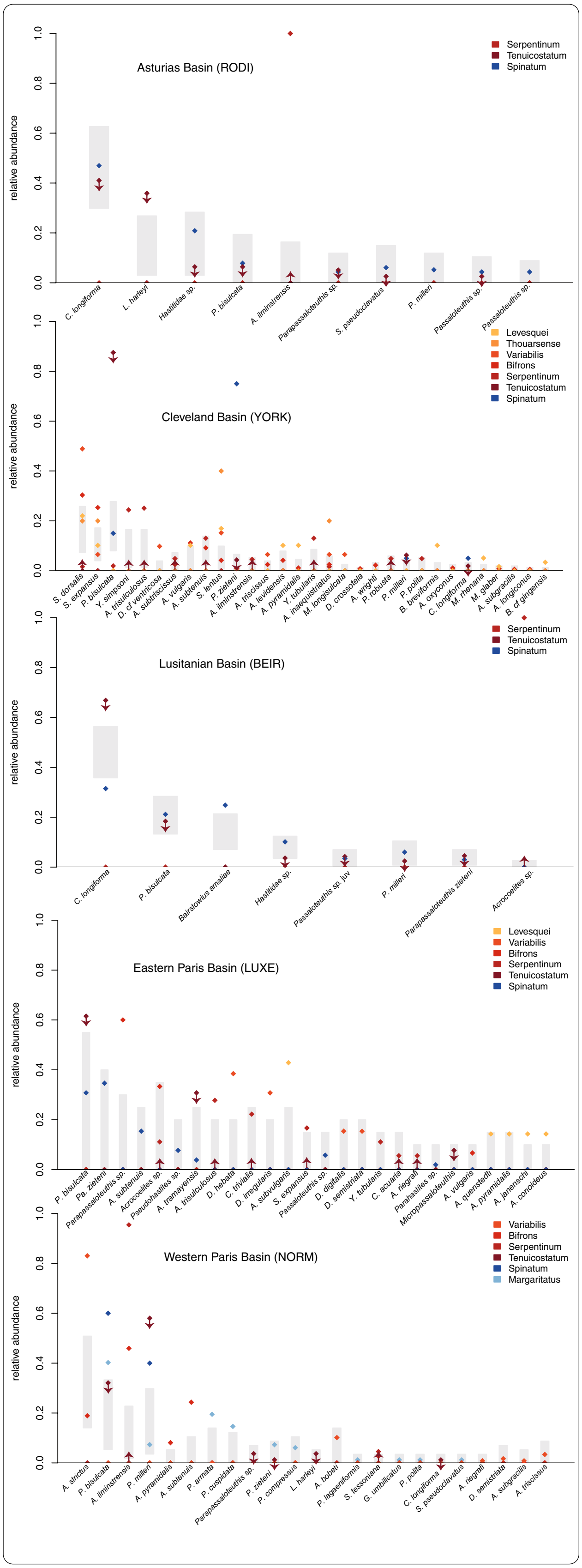


Fig. 4 Results of the SIMPER analyses when comparing the Spinatum–Tenuicostatum as well as the Tenuicostatum–Falciferum Zones. Eight species explaining the largest shifts in dissimilarity are depicted

in species relative abundances happen across both, the PToB and the T-OAE, the more drastic community composition shifts are seen across the latter (Serpentinum Zone). The species that dominate the communities after the PToB vary between the southern locations (BEIR, RODI) and the northern locations (NORM, YORK). *C. longiforma* and *Hastitidae* sp. dominate the earliest Toarcian communities in the Lusitanian (BEIR) and Asturian (RODI) Basins, respectively. In the Western Paris (NORM) and Cleveland (YORK) Basins the dominating species after the boundary are both from the *Passaloteuthis* genus (*P. milleri* (NORM), *P. bisulcata* (YORK)).

Additionally, the shifts in relative abundances across the T-OAE are more drastic in the more southern localities, where a single, new species makes up (almost) the entire assemblage in the Serpentinum Zone, than in the more northern basins (*Acrocoelites ilminstrensis* in the Lusitanian Basin, *Lissajousibelus harleyi* in the Asturias Basin). This pattern is similar but less pronounced in the intermediate basins Causses and the Western Paris Basin, in which newly appearing species dominate the



◀ **Fig. 5** Results of the Bootstrap method for various basins. Only points corresponding to zones falling outside the grey boxes reflect significant changes in relative abundance of species. Arrows highlight in which direction to look for the relative abundance calculations when going from the Tenuicostatum (post-Pli-Toa) to the Falciferum Zone (post-TOAE). An enlarged version can be found in the supplementary material (Fig. S9)

assemblage in the Serpentinum Zone, but not at a hundred percent (*Acrocoelites subtenuis* in Causses and *A. ilminstrensis* in the Western Paris Basin). While the species in the community also change entirely in the northernmost basin, Cleveland (YORK), the Serpentinum Zone is not only dominated by a single species here, but a cluster of species that are very abundant after the T-OAE (*Youngibelus tubularis, Y. simpsoni*, *Acrocoelites trisulculosus*). *Simpsonibelus dorsalis* also appears first in the Serpentinum Zone, after which its abundance grows steadily, leading to it dominating the community in subsequent zones.

Body size

At most localities, the size changes within assemblages are dominated by within-lineages changes, including at the Pliensbachian–Toarcian transition, while taxonomic turnover seems to play a lesser role in driving patterns with some exceptions (Fig. 6). The changes in body size distribution from the Spinatum to Tenuicostatum Zone are not markedly different from those between other consecutive zones (Margaritatus–Spinatum, Falciferum–Bifrons, Bifrons–Variabilis, Variabilis–Thouarsense, Thouarsense–Pseudoradiosa). However, the appearance and/or disappearance of taxa seem to have large effects on median body size distribution, particularly during the T-OAE (Fig. 7). During this event, the effect of large species appearing outweighs the effect of smaller taxa disappearing, which typically leads to an increase in body size during the T-OAE at the 5 studied basins.

Discussion

Diversity

Adding more sub-Mediterranean data did not markedly change the observed impact of the Pliensbachian–Toarcian crisis on belemnite diversity. This is also consistent with analyses of rarified diversity of individual localities based on relative abundance of BEIR, RODI and YORK (Rita et al., 2021). However, most localities we could study in detail show a decrease in diversity during the T-OAE, whereas some NW-European localities show an increase in diversity that is also seen at the scale of the NW-Tethys analyses.

When focusing on diversity reported from individual regions with a reasonable coverage of the Spinatum

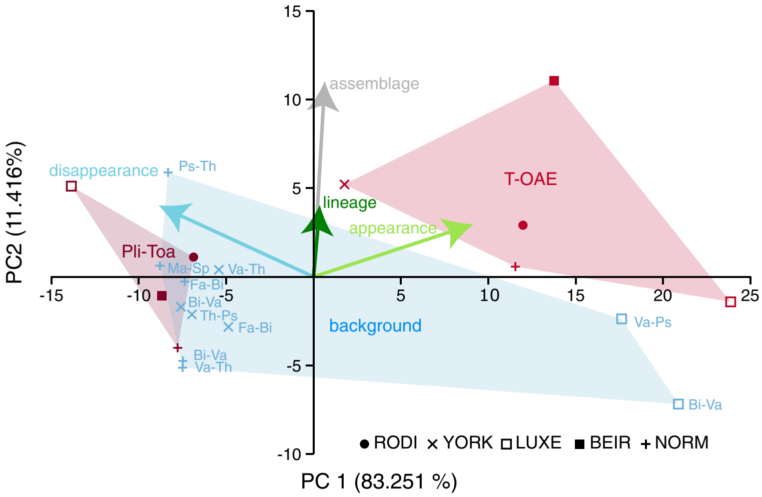


Fig. 6 PCA biplot plotting the median size changes between assemblages attributable to zones and their components (assemblage: size changes seen within entire assemblage; lineage: size changes within lineages crossing the boundary; appearance: size changes drive by specimens appearing; disappearance: size changes driven by specimens appearing). Observations are grouped based on the transition from Spinatum–Tenuicostatum Zone (Pli-Toa crisis), Tenuicostatum–Serpentinum Zone or Serpentinum–Bifrons Zone (T-OAE) and all others (background)

and Tenuicostatum Zone, there is a minor decrease in rarefied richness in most localities and the dominant reported species within or across regions also do not markedly differ. In the NW-Tethys-scale analysis, the diversity increases from the Tenuicostatum to Serpentinum Zone. This is consistent with the rarefied diversity analysis of some individual localities (e.g., YORK).

Taxonomic turnover

The impact of the Toarcian Oceanic Anoxic Event on diversity at the zonal level can be divided between some regions where diversity markedly drops (e.g., Asturian Basin, Lusitanian Basin), and some others in which diversity increases. However, even for the latter, we note that diversity decreases at the subzone and/or bed level across the T-OAE (Rita et al., 2021). This suggests that there is an impact of the Toarcian Oceanic Anoxic Event, but that it is blurred on the zonal level by the subsequent appearance of new taxa. Ullmann et al. (2014) argued that *Acrocoelites* might have been better adapted to warmer oxygenated surface waters and radiated after the T-OAE with some species returning to periodically oxygenated bottom water habitats.

Further research is, however, necessary to disentangle if this is a genuine pattern or rather a sampling issue, as the record of belemnite becomes sparse in some regions (e.g., Lusitanian Basin, Rif Mountains) during the Serpentinum Zone. Still, the species and patterns reported are remarkably similar in several basins which might suggest that southern areas are more heavily impacted by the warming events than the northern European domains due to the northward circulation of hot Tethyan waters. Irrespective of the changes in diversity, there is good support for a taxonomic turnover from the Tenuicostatum to the Serpentinum Zone, with the dominant taxa changing within basins (regionally) and across the NW-Tethys. This is consistent with our current and previous investigations of compositional similarity which focused on well-sampled localities (Rita et al., 2021).

Body size

Our analyses support that body-size responses at the Pliensbachian–Toarcian boundary are mainly driven by within-lineage changes in particular regions (e.g., Asturian Basin, Western Paris Basin, Lusitanian Basin) as opposed to the T-OAE which is mainly driven by taxonomic turnover in all investigated localities. In the case of the Pliensbachian–Toarcian boundary, changes in some basins are evocative of a Lilliput effect s.l. (Morten & Twitchett, 2009; Rita et al., 2019; Twitchett, 2007) within individual lineages (Lusitanian Basin, Western Paris Basin), but preliminary data in other basins rather show an increase in body size within lineages crossing the boundary (e.g., Asturian Basin, Eastern Paris Basin). The best studied example (BEIR) provides evidence for a size decrease within assemblages, which is driven by the decrease in adult size in the dominant species (Nätscher et al., 2021; Rita et al., 2019). On the other hand, preliminary data from the Asturias Basin and Eastern Paris Basin rather document an increase in body size within the same individual lineages crossing the boundary suggesting a pre-TOAE decline in body size is not a general pattern

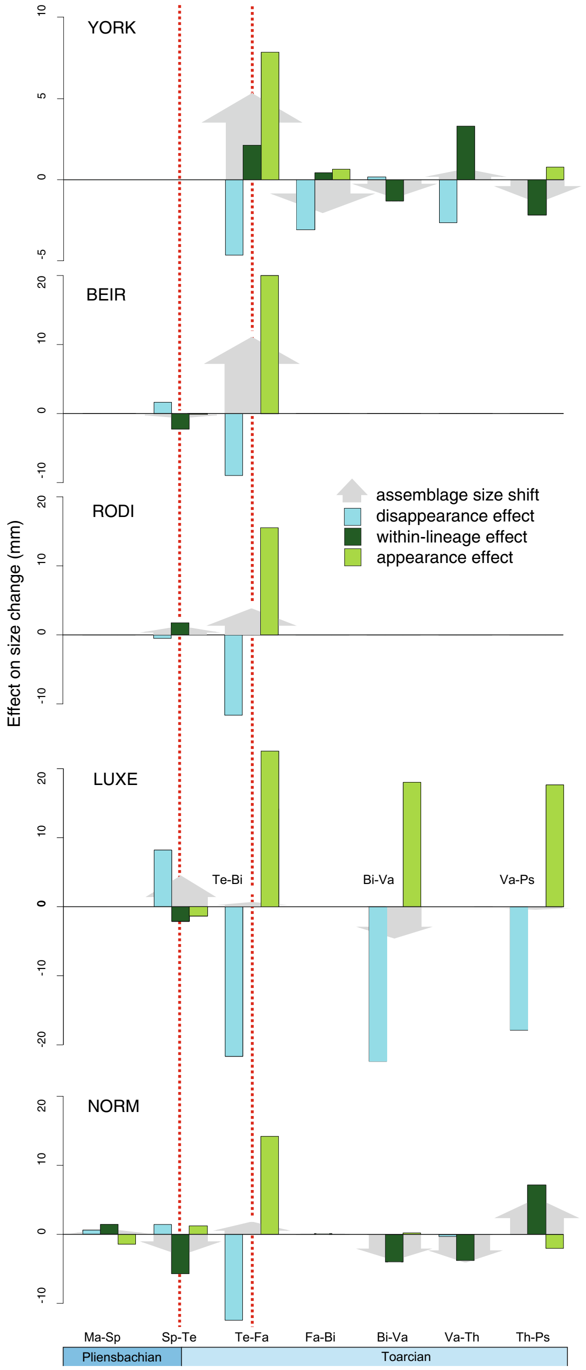


Fig. 7 Assemblages body size changes and size changes decomposed into within lineage, disappearance and appearance components for the Cleveland (YORK), Lusitanian (BEIR), Asturian (RODI), Eastern Paris (LUXE) and Western Paris (NORM) basins. These are based on all measured specimens rather than species means. Dotted vertical red lines indicate the two pulses of the second-order Toarcian crisis

across the NW-Tethys (Nätscher et al., 2021; Piazza et al., 2019; Rita et al., 2019). It is at the moment unclear if this reflects the fact that these northern European assemblages were less severely impacted by the warming event than the more southernly located regions as suggested by some models (Dera & Donnadieu, 2012; Piazza et al., 2019; Rita et al., 2019) or rather lower sampling of size measurements and ontogenetic stages from those localities. Other authors have attributed the success of particular lineages (e.g., belemnite *Acrocoelites* or brachiopod

Soaresirhynchia) in the aftermath of the T-OAE to their ability to better cope with a shift in habitats (Piazza et al., 2020; Ullmann et al., 2014). However, the impact of migration and shifts in habitats are currently difficult to assess as detailed abundance and size distribution for ontogenetic stages is only available for Peniche (BEIR). Preliminary observations also run counter to suggestion that belemnite species markedly changed their habitat preferences from the Pliensbachian to the Toarcian—at least in Peniche—and might rather argue for clear preferences of particular lineages to colder or warmer habitats (Nätscher et al., 2021).

In the case of the switch from the Tenuicostatum to Serpentinum Zone, the changes in median size are mainly driven by taxonomic turnover. This is not surprising as our analyses support that the species composition changes dramatically in well-studied localities as well as in the analysis at the scale of the NW-Tethys. In most cases, this leads to an increase in median body size when the increase relates with assemblages, except for the Western Paris Basin. This does not necessarily mean that some species were not decreasing in size, but that the appearance of new species and disappearance of previous species had a dominant impact. The influence of incomplete sampling on these patterns, however, still needs to be investigated. There are also marked differences among localities, particularly between NW European and (sub)Mediterranean localities. The transition from the Spinatum to the Tenuicostatum Zone is usually better documented in the (sub)Mediterranean localities (Morard et al., 2003; Rita et al., 2021), where belemnites become scarce or entirely disappear during the Serpentinum Zone. In the data available with a higher stratigraphic resolution from the Toarcian in the Lusitanian Basin (Rita et al., 2019), there is a tendency for larger juveniles to become dominant, while small juveniles as well as large adults become rare towards the end of the Tenuicostatum Zone, which leads to an increase, rather than a decrease, in median body size before the T-OAE and in its immediate aftermath. However, sparse sampling, as well as difficulties determining smaller individuals in smaller samples could also contribute to this pattern. The impact of preferential sampling of larger or smaller individuals on patterns needs to be further investigated. It underlines the need for further paleobiological datasets including both relative abundance and body size even in previously studied regions (e.g., Morocco, Southern Germany) and higher resolution data to fully understand the drivers behind these patterns. To resolve this issue, we recommend to sample in high stratigraphic resolution (bed to subzone level) as well as standardize collecting within samples by area (see Rita et al., 2019) or weights as well as investigate shifts in the distribution of ontogenetic stages (Zakharov et al., 2014). However, all presently available evidence and consistency between different regions (irrespective of diversity trajectories) and sampling regimes support an increase of median body size from the Tenuicostatum to the Serpentinum Zone coinciding with marked taxonomic turnover. The pattern of increase rather than decrease in median body size is reminiscent of similar patterns reported from various mass extinction events at coarser stratigraphic resolution (Payne et al., 2016). These observations might hint that both origination and extinction dynamics play a large role in driving body size distribution in assemblages (Monarrez et al., 2021) surrounding such events then commonly embraced (Rego et al., 2012)—even at more highly resolved spatial (regional) and temporal (Chronozone) scales.

Conclusions

Although similar climatic factors have been implicated in both pulses, our analyses support a differential response of belemnite diversity and size distribution to the Pliensbachian–Toarcian Boundary event (PToB) than to the T-OAE. A focus on regions with well-sampled boundary intervals shows support for a slight decrease in diversity in most regions across the Pliensbachian–Toarcian boundary (PToB). Belemnite richness markedly drops in some localities across the T-OAE, while in some others and at the scale of the NW-Tethys, there is an increase in diversity from the Tenuicostatum to Serpentinum Zone. All in all, we found no marked changes in the species composition across the Pliensbachian–Toarcian boundary. In contrast, there is a marked shift from *Passaloteuthis*/*Cata teuthis*/*Parapassaloteuthis* dominated assemblages to *Acrocoelites*-dominated assemblages across the T-OAE throughout the NW-Tethys, suggestive of high extinction and origination rates (and therefore taxonomic turnover). Our analyses suggest a decrease in median body size in assemblages in few of the best-studied localities, during the Pliensbachian–Toarcian transition. We find support for a marked taxonomic turnover coinciding with an increase in median size within assemblages across the T-OAE in the five basins we could study in detail. This highlights the importance of extinction and origination dynamics in driving shifts in body size distribution (Monarrez et al., 2021).

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-021-00242-y.

Additional file 1: Fig. S1. Raw species diversity curves for the localities studied in detail. Asterisk(*) refers to updates made in this study compared to Neige et al. (2021).

Additional file 2: Fig. S2. Most commonly reported species in localities from Spinatum, Zone Tenuicostatum and Serpentinum Zones and the corresponding cumulative curve (in red). Illustrations of the 6 most common species are added next to them.

Additional file 3: Fig. S3. Belemnite sampling coverage computed for a standardized set of 16 localities for each time bin, together with the 95% confidence intervals from Neige et al. (blue) and this study (orange). Chronostratigraphic framework as in Fig. 2.

Additional file 4: Fig. S4. Cumulative dissimilarity Margaritatus–Spinatum Zone (999 permutations)

Additional file 5: Fig. S5. Cumulative dissimilarity Serpentinum–Bifrons Zone (999 permutations)

Additional file 6: Fig. S6. Cumulative dissimilarity Bifrons–Variabilis Zone (999 permutations)

Additional file 7: Fig. S7. Shepard diagram. Relationship between NMDS ordination distance and original observed distance. NMDS ordination was undertaken on an occurrences per species matrix.Anosim analysis results.

Additional file 8: Fig. S8. Anosim analysis results. Between represents the difference between zones; others are within zones; the greater the distance is, the greater the difference is; and the thickness is proportional to the sample size.

Additional file 9: Fig. S9. Results of the Bootstrap method for various basins including the Causses Basin. Only points corresponding to zones falling outside the grey boxes reflect significant changes in relative abundance of species.

Additional file 10. SupFile 1. Results of ANOSIM analyses.

Additional file 11. SupFile 2. Results of SIMPER analyses.

Additional file 12. SupFile 3. Results of Rego Size Analyses.

Additional file 13. SupFile 4. Raw Diversity data (relative abundance) used for regional rarefied richness analyses.

Additional file 14. SupFile 5. Raw Diversity data (occurrences) used for NW Tethys rarefied richness analyses.

Additional file 15. SupFile 6. Raw Size data used for the Rego Size analyses.

Additional file 16. SupFile 7. R-script and files used for our analyses (as a zip file).

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Authors' contributions

KDB designed the study. KDB and PN contributed main analyses and wrote manuscript. KDB, PN and PR contributed main data. PR, EF and PN contributed additional analyses. JB, GD, LVD, ZH, PL, JGR, LP, CÜ and RW contributed field and/or specimen data. All 14 authors contributed to the text, proofread various versions of the text, and approved it. All authors read and approved the final manuscript.

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Availability of data and materials

Most of the belemnite material has been described in previous taxonomic treatments. Rare unpublished material follows the assignments as used in the primary literature and as revised by Neige et al. (2021). All the associated data, results of the analyses as well as code can be found in the Additional files 10, 11, 12, 13, 14, 15 and 16.

Declarations

Competing interests

The authors declare no competing interests.

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