New range data for marine invertebrate species across the early Toarcian (Early Jurassic) mass extinction

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Abstract: We have reinvestigated the marine mass extinction interval that occurred during the early Toarcian, which was a time of widespread marine anoxia. The ranges of marine benthic invertebrates are significantly altered using new observations from the Cleveland Basin, UK. Goniomya rhombifera is reported for the first time from the Whitby Mudstone Formation and together with an increased epifaunal bivalve diversity indicates a brief, relatively oxygenated period towards the end of the event. The new data, together with published results, suggest three apparent extinction horizons on a global scale; the first is just above the Pliensbachian–Toarcian boundary, and the following two are in the semicelatum ammonite Subzone. As a result of the Signor–Lipps effect there may be only one, or possibly two, true extinctions. The youngest extinction horizon coincides with the first of the abrupt carbon isotope shifts that characterize this interval, and with increases in sea surface temperature, continental weathering rates, and seawater anoxia. Pseudomytiloides dabis is the only abundant benthic macroinvertebrate during the most hostile environmental conditions but it and all other benthic species are almost entirely absent for many thousands of years immediately after each abrupt negative carbon isotope shift.

Supplementary material: A compilation of the Late Pliensbachian and Early Toarcian marine biotic changes and a discussion of the systematics of the key faunal elements are available at http://www.geolsoc.org.uk/SUP18353.

The early Toarcian (Early Jurassic) was a period of sudden and severe global environmental change. The interval was characterized by the worldwide accumulation of organic-rich facies (Fig. 1a), an observation that has led to its being described as an Oceanic Anoxic Event (Jenkyns 1988, 2003). A large, relatively short-lived negative carbon isotope excursion of c. 7‰ in marine organic matter is observed in samples spanning the early Toarcian lithologies of the upper Dactylioceras semicelatum and Harpoceras exaratum subzones from Europe, Canada and Argentina (Fig. 2; Rohl et al. 2001; Cohen et al. 2004; Kemp et al. 2005; van Breugel et al. 2006; Al-Suwaidi et al. 2008; D. R. Gröcke, pers. comm.). Contemporary marine carbonates from Europe show a negative carbon isotope excursion of up to 6‰ (Hesselbo et al. 2007; Suan et al. 2008a; Hermoso et al. 2009). The negative carbon isotope excursion has also been found in fossilized wood (Hesselbo et al. 2000, 2007; McElwain et al. 2005), indicating that the carbon isotope excursion affected the entire ocean–atmosphere system. Taken together, the high levels of organic carbon accumulation and the pronounced negative carbon isotope excursion indicate that the global carbon cycle was severely disrupted at that time.

Oxygen isotope and Mg/Ca ratios provide proxy evidence for a large contemporaneous rise of 7–13 °C in mid-latitude seawater surface temperatures (McArthur et al. 2000; Bailey et al. 2003; Gomez et al. 2008; Suan et al. 2008a), and marked changes in the marine Sr- and Os-isotope records indicate that the rate of continental weathering increased abruptly (Cohen et al. 2004). Recent Mo-isotope data (Pearce et al. 2008; Fig. 2) suggest that the areal extent of seawater anoxia expanded by an order of magnitude at that time and may have encompassed a large proportion of the world’s continental shelves. Several European records of this event have yielded high concentrations of various biomarkers (aryl isoprenoids (Schwark & Frimmel 2004), isorenieratane (Fig. 2; Schouten et al. 2000; van Breugel et al. 2006), methyl isobutyl maleimide and high molecular weight porphyrins (Pancost et al. 2004)) that are derived from accessory photosynthetic pigments of phototrophic anoxygenic bacteria, the Chlorobiaceae, and are indicative of photic zone euxinia.

Sepkoski (1986) defined a mass extinction as ‘any substantial increase in the amount of extinction (i.e., lineage termination) suffered by more than one geographically widespread higher taxon during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing diversity’. In contrast, regional extinction of a taxon occurs at a local level only and it may serve as a nucleus for recovery. The environmental changes that occurred during the early Toarcian coincided with mass extinctions in both the terrestrial (Benton 1995) and marine realms (Riegraf 1985; Benton 1995; Little 1995, 1996; Aberhan & Fursich 1996; Hori 1997; Hylton 2000; Palliani et al. 2002; Erba 2004; Gahr 2005; Zakharov et al. 2006). It has been estimated that during the Toarcian Stage c. 5% of marine families (Benton 1995) and c. 26% of marine genera (Raup & Sepkoski 1986) became extinct, significantly exceeding background extinction levels. In comparison, 15% of marine families and 50% of marine genera become extinct at the Cretaceous–Paleogene boundary (Raup & Sepkoski 1986). The mass extinction interval in the marine realm spans two ammonite zones representing a time interval of c. 1 Ma (Pálffy et al. 2002; Gradstein et al. 2004).

The present study has concentrated on Toarcian sedimentary deposits that accumulated in the Cleveland Basin and are now exposed near Whitby, UK (Fig. 1c). The upper Pliensbachian and
lower Toarcian of the Cleveland Basin comprise the Cleveland Ironstone Formation and the Whitby Mudstone Formation, respectively (Howarth 1955, 1962, 1973). The Whitby Mudstone Formation is subdivided into three members: the Grey Shales Member, the Mulgrave Shales Member and the Alum Shale Member (Fig. 3). The Whitby Mudstone Formation is predominantly composed of pale- to dark-grey mudstones that were deposited in fully marine conditions below storm wave-base. The mudstones contain occasional bands of laterally persistent calcitic or sideritic concretions. These lower Toarcian facies were examined at a high stratigraphical resolution and the range, abundance and size of the benthic invertebrate fauna were recorded (presentation and discussion of species size data are outside the scope of this paper, and will be presented elsewhere). The species ranges and abundance are correlated with geochemical proxy data from the same section. This study has also reassessed the worldwide distribution of macrofaunal and microfloral and -faunal changes associated with the palaeoenvironmental event using existing literature. The alterations to species ranges that we document here contribute to the interpretation of the late Pliensbachian to early Toarcian extinction interval in the Cleveland Basin and add to our understanding of the prevailing palaeoenvironmental conditions.

**Late Pliensbachian and early Toarcian extinctions of marine biota**

Previous studies of marine fauna from late Pliensbachian to early Toarcian age successions have documented significant extinctions within many taxonomic groups, and major changes in the relative abundance of calcareous nannofossil and dinoflagellates, from a wide range of palaeogeographical localities in both the Boreal and the Tethyan realms (Figs 1a and 4). These extinctions, and changes in the relative abundance of calcareous nannofossils and dinoflagellates, occur at several different stratigraphical levels in both realms, indicating a complex pattern of extinction. Several researchers have suggested that the mass extinction may be divided into at least two phases; at the Pliensbachian–Toarcian boundary and in the *semeleatum* Subzone (Little 1996; Harries & Little 1999; Cecca & Macchioni 2004; Wignall *et al*. 2005; Wignall & Bond 2008).

Differences between the timing of significant relative abundance changes or extinctions for the Toarcian are in some cases a consequence of either poor biostratigraphical resolution or variable sedimentation rates, or both. Additionally, some strata may be absent. These uncertainties are depicted in Figure 4 by dashed lines, the upper end of the dashed line indicating the youngest possible range. In NW Europe the biostratigraphy is well documented (Howarth 1955, 1962, 1973; Page 2004) but this is not the case for all geographical regions.

There are extinctions in the microfossil groups (Fig. 4). Amongst the calcareous nannofossils and dinoflagellates only one extinction is recorded but large decreases in their relative abundances are observed (Fig. 4; Prauss *et al*. 1991; Palliani & Riding 1999; Palliani *et al*. 2002; Erba 2004; Tremolada *et al*. 2005). The evolution of the first planktic foraminifers is believed to have resulted from the early Toarcian Oceanic Anoxic Event (Hart *et al*. 2003).
The lower Toarcian rocks within the Cleveland Basin are typical of the organic-rich mudrocks that were deposited across NW Europe (Fig. 1b) at that time. These mudrock facies contain a benthic faunal assemblage of relatively low diversity that was largely dominated by ammonite conchs, belemnites and epifaunal bivalve species. Faunal assemblage composition is very similar across NW Europe, with four bivalve species in most cases dominating the lower Toarcian succession (Riegraf et al. 1984; Little 1995; Roehl et al. 2001). These species are *Bositra radiata* (Goldfuss) (Fig. 5a), *Pseudomytiloides dubius* (Sowerby) (Fig. 5b), *Meleagrinella substriata* (Muenster) (Fig. 5c) and *Bositra buchi* (Roemer) (Fig. 5d).

Harries & Little (1999) interpreted the pattern of marine invertebrate species ranges from this study through the *semicelatum*, *exaratum* and lower *falciferum* subzones of the Whitby Mudstone Formation. Abundance data include individuals from all size classes. Carbon isotope data are from Kemp et al. (2005); carbon isotope shifts A–D are from Kemp et al. (2005) and Cohen et al. (2007). Mo-isotope and abundance data are from Pearce et al. (2008). Isorenieratane (μg g⁻¹ total organic carbon (TOC)) data are from Dotternhausen, Germany (Schouten et al. 2000). Very poorly fossiliferous intervals are shown in grey. (For species codes, and details of extinction steps and horizons see Fig. 3.) Between stratigraphical height −71 cm and 694.5 cm there are no *B. radiata*. The succession was searched in detail and each stratigraphical level is marked by a point at zero abundance. References for stratigraphical logs are as for Figure 3.

The Cleveland Basin

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Harries & Little (1999) interpreted the pattern of marine invertebrate species ranges from this study through the *semicelatum*, *exaratum* and lower *falciferum* subzones of the Whitby Mudstone Formation (just below the *apyrenum–hawskerense* subzone boundary) where five out of 35 species disappear; (2) approximately half a metre above the Pliensbachian–Toarcian Stage boundary (within the *paltum* Subzone) where 10 out of 39 species become extinct; (3) near the middle of the *semicelatum* Subzone where 18 out of 30 species disappear; (4) near the top of the *semicelatum* Subzone boundary where seven out of 13 species become extinct. Step (3) of Harries & Little (1999) contains the highest proportion of fauna that became extinct and was interpreted as the main extinction event by Harries & Little (1999). Benthic fauna were more severely affected than were pelagic fauna, with 87% of benthic species and all of the infauna becoming extinct (Little 1996). Diversity levels did not begin to increase until much later towards the middle of the Toarcian (when the *bifrons* Zone was deposited); this is also when the infaunal organisms are recorded to reappear in NW Europe (Rieggraf 1985; Little 1996; Fursich et al. 2001; Rohl et al. 2001; Schmid-Rohl et al. 2002). These assemblages are dominated by a high abundance of opportunists.
Materials and methods

Benthic macro-fossil range data were collected from the Whitby Mudstone Formation at five field sites: Hawsker Bottoms [NZ 947079], Port Mulgrave [NZ 799178], Saltwick Bay [NZ 916111], Kettleness [NZ 835160] and Ravenscar [NZ 981023] (Fig. 1c). Overall, the formation is relatively poorly fossiliferous and shells tend to occur in pavements (as defined by Kidwell et al. 1986) at discrete stratigraphical levels. The top 4 m of the Grey Shales Member (Figs 3 and 4) and all of the Mulgrave Shales Member were examined for fossil occurrences at sub-centimetre stratigraphical resolution in the extensive foreshore exposures as well as in the sea cliffs. The lower 10 m of the Grey Shales Member and the Alum Shale Member were examined on a decimetre scale.

The δ¹³Corganic data of Cohen et al. (2004) and Kemp et al. (2005) were used to investigate the links between the benthic faunal species distributions and changes in the carbon cycle. The negative carbon isotope excursion occurred in four abrupt shifts of c. 2–3‰ that have been designated ‘A’ to ‘D’ (Kemp et al. 2005; Cohen et al. 2007). An astronomical time scale was established for this section by Kemp et al. (2005) and Kemp (2006), yielding an estimated duration of c. 295 ka for the entire negative carbon isotope excursion (Kemp 2006; Cohen et al. 2007). Suan et al. (2008b), on the basis of sections in Peniche, Portugal and Dotternhausen, SW Germany, suggested a longer duration of c. 900 ka for the entire negative carbon isotope excursion. However, the detailed correlation between the section in Portugal, the condensed section in Germany and the Yorkshire sections is unclear, and the section in Portugal contains mass flow deposits making it poorly suited for time series analysis. The use of the time scale of Suan et al. (2008b) is therefore thought to be inappropriate for the Yorkshire section.

The invertebrate fossil range data for this study are based on observations made at the same exposures that were used for the earlier geochemical studies (Cohen et al. 2004; Kemp et al. 2005; Kemp 2006; Pearce et al. 2008). The fossil range data have been correlated at a centimetre stratigraphical precision relative to the positions of the geochemical samples.

Non-parametric confidence intervals for the key species (Table 1) have been calculated for this study and for the range data of key species of Little (1995). Confidence intervals were calculated using the program ‘Past.exe’ (Hammer et al. 2001) and the method of Marshall (1994). It was not possible to calculate confidence intervals for some species because of insufficient data (fewer than seven fossil horizons; Marshall 1994) or because the species range continues outside the section studied.

The average stratigraphical spacing at which abundance data for P. dubius and B. radiata (Fig. 2) were collected at was 4.5 cm through the upper Grey Shales Member and the lower half of the Mulgrave Shales Member (bed 33 to the middle of bed 43; Fig. 2). Shell abundances were counted within a 20 cm × 20 cm area of bedding plane.

Results

Eight bivalve species (Fig. 5), one brachiopod species and one crinoid species were found in the top c. 2 m of the Grey Shales Member, through the entire Mulgrave Shale Member and in the basal 11 m of the Alum Shale Member (Fig. 3). The new range data for these species are as follows (Figs 2 and 3, and Table 1).

(1) Individuals of the bivalve Goniatrya rhombifera (Goldfuss) (Fig. 5e) were found between 65 cm below and 11 cm above the base of bed 39 (Fig. 3, the Top Jet Dogger of Howarth (1962)).

(2) Meleagrinella substratiata was observed between 14 cm above the middle of the nodules that form bed 11 and the top of bed 51 (Fig. 3).

(3) Bositra radiata was found between 29.5 cm above the middle of the nodules that form bed 30 and up to 2 cm above the top of bed 40.

(4) Bositrus buchi was recorded between 12 cm below the base of bed 39 and 188 cm above bed 48.

*Fig. 3. Stratigraphical log for the Yorkshire section from Kemp (2006), except for the basin 5 m, which are from this study and Hesselbo & Jenkyns (1995); ammonite biostratigraphy is from Howarth (1962, 1973). The units informally referred to as the ‘Jet Rock’ and the ‘Bituminous Shales’ are those represented by the exaratum and falciiferum subzones, respectively. Range data: the right-hand column for each species shows the data re-plotted from Little (1995) (squares joined by continuous lines); new data from this study (diamonds) are displayed in the left hand of the column for each species. Dashed horizontal lines: four extinction steps 1–4 proposed by Harries & Little (1999). The stratigraphical locations of the global extinction levels identified in this study are labelled i–iii. In Yorkshire, the number of species extinctions/number of species at these levels are: (i) 9/30; (ii) 14/25; (iii) 6/16. Species codes: Bivalves: 1, Antiquilima sp.; 2, Palmoxytoma cygnipes (Young and Bird); 3, Gryphaea (Gryphaea) gigantea (J. de C. Sowerby); 4, Mesosaccella galatea c. exaratum (Simpson); 5, Gryphaea (Bilobissa) sportella (Dumortier); 6, Macromya cardioidea (Phillips); 7, Pholadomya ambigua Sowerby; 8, Gresslyia intermedia (Simpson); 9, Plicatula spinosa (J. Sowerby); 10, Pinna folium Young and Bird; 11, Modiolus scalprum J. Sowerby; 12, Entolium (Entolium) lunare (Roemer); 13, Palaeanucula navis (Pitte); 14, Eutrapelium cucculatum (Goldfuss); 15, Pleuroceras costata (Young and Bird); 16, Grammatodon (Grammatodon) insous Melville; 17, Niaciella striatoulcata (Roemer); 18, Nuculana sp. A.; 19, Pseudopezeten (Pseudopezeten) equivalvis (J. Sowerby); 20, Pseudolimina acuteocrusta (Münster); 21, Paraminoceras sp. A; 22, Protocardia truncata (J. de C. Sowerby); 23, Nucinella sp.; 24, Bositrus radiata (Goldfuss); 25, Pseudomytiloides dubius (Sowerby); 26, Meleagrinella substratiata (Münster); 27, Goniomya rhombifera (Goldfuss); 28, Camptonectes (Camptonectes) auritus (Schlotheim); 29, Oxytoma inequivalve (J. Sowerby); 30, Bositrus buchi (Roemer); 31, Liostrea hisingeri (Nilsson); 32, Dacyrotyla ovum (Sowerby). Brachiopods: 33, Lingularia longiovensis (Terquem); 34, Lobothyris punctata (J. Sowerby); 35, Tetranchynchia tetrahedra (Sowerby). Gastropods: 36, Procerithium sp. A; 37, Ptychomphalus expansus (J. Sowerby); 38, Oolina clevelandiana (Tate); 39, Katosira blainwillei (Münster). Crinoids: 40, Pentacrinites dichotomus (McCoy); 41, Balanoocrinus donovani Simms; 42, Isocrinus basaltiformis (Miller); 43, Scirocrinus subangularis (Miller). Belemnites: 44, Pseudohastites longiformis (Blake); 45, Parapassaloteuthis zieteni (Mayer-Eymar); 46, Passaloteuthis milleri (Phillips); 47, Passaloteuthis bisulcata (Blainville); 48, Acrocoelites (Praeapachyteuthis) tristriatus (Simpson); 49, Youngibelus tubularis (Young and Bird); 50, Parapassaloteuthis polita (Simpson); 51, Acrocoelites (Acrocoelites) riegrafyi Doyle; 52, A. (A.) suburbicrus Kolb; 53, A. (A.) subtenus (Simpson); 54, A. (Odontobulus) vulgaris (Young and Bird); 55, Simpsoinosbals (Phillips); 56, A. (Praepachyteuthis) inaequistriatus (Simpson); 57, A. (O.) triscissus (Janensch). Ammonites: 58, Pleuroceras apyrenum (Buckman); 59, Pl. hawksberenense (Young and Bird); 60, Dactyloceras (Orthactyloceras) crosebyi (Simpson); 61, D. (O.) clevelandicum Howarth; 62, D. (O.) tenuicostatum (Young and Bird); 63, D. (O.) semiculatum (Simpson); 64, Tilonictes antiquum (Wright); 65, Elegantoceras elegantulum (Young and Bird); 66, Lytoceras crenatum (Buckman); 67, Harpoceras exaratum (Young and Bird); 68, H. elegans (J. Sowerby); 69, Hildaites murely (Moxon); 70, Nodicoeloceras inrasatus (Simpson); 71, H. falceferum (J. Sowerby); 72, Ovaticeratida ovatum (Young and Bird); 73, Dactyloceras sp.; 74, Phylloceras heterophyllum (J. Sowerby); 75, D. commune (J. Sowerby). Serpulids: 76, Serpula sp. A.*
Fig. 4. Summary of Early Toarcian micro- and macro-fossil extinctions and decreases in relative abundances from the Boreal and Tethyan realms. Black lines, pelagic taxa; grey lines, benthic taxa; open boxes, change in relative abundances of calcareous nannofossils (calc. nannofossils) and/or dinoflagellates. Ammonite biozonation and biostratigraphical correlation between faunal provinces: Subboreal, particular index species; with the exception of the ‘semicelatum II’ division of the Mediterranean and Submediterranean, which is defined by first occurrence of abundant *clevelandicum* Subzone). Extinction levels and decreases in relative abundances are plotted as the minimum stratigraphical level at which the extinction occurs and the uncertainties are shown by dashed lines. Where uncertainty has not been indicated in the literature a minimum value of half an ammonite subzone is given. Where the position of the extinction horizon has been established at the stage boundary only, with no zonal biostratigraphical resolution given, large uncertainties have been assigned. Three possible global extinction horizons (i–iii) based on evidence in this study are indicated. Proportion of extinctions within each group (taken from the literature) is given at the base of the figure; NQ, not quantified; AC, an unquantified change in the assemblage composition occurred. For dinoflagellate cysts and calcareous nannofossils the decrease in relative abundance (%) is provided. Geographical localities: 1, NE Siberia (Nikitenko & Shurygin 1992; Zakharov et al. 2000; Cecca & Macchioni 2004); 10, North Spain (Garcia Joral & Goy 2000; Cecca & Macchioni 2004; Gahr 2005; Tremolada et al. 2005); 13, Ilminster, Southern England (Boomer 1992); 14, Portugal (Boomer et al. 1998; Gahr 2005); 15, NW Caucasus (Ruban 2004; Ruban & Tyszka 2005); 16, Italy (Palliani & Riding 1999; Cecca & Macchioni 2004; Erba 2004); 17, Southern Spain (Cecca & Macchioni 2004); 18, Morocco (Cecca & Macchioni 2004); 19, Japan (Hori 1997); 20, Southern Andes (Riccardi et al. 2003; Aberhan & Fursich 1996).

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(5) *Camptonectes auritus* (Schlotheim) was recorded as occurring only once at 31 cm below the base of bed 39.

(6) *Pseudomytiloides dubius* was found from 10 cm below the top of bed 1 up to 45 cm below the base of bed 50.

(7) *Dacryomya ovum* (Sowerby) occurred from 90 cm below to 20 cm above bed 52.

(8) The brachiopod *Lingularia longicostata* (Terquem) was found between the base of bed 49 and up to 153 cm above.

(9) The crinoid *Pentacrinutes dichotomus* (McCoy) was found between 35 cm below the top of bed 31 and 71 cm below the top of bed 42.

In the lower part of the Grey Shales Member, a further eight bivalve species were found in addition to the species described above (Fig. 3). Fossils are generally rare in these beds but some abundant horizons occur. *Pholadomya ambigua* (Sowerby) was found in bed 28 of the *paltum* Subzone and *Picatudra spinosa* (J. Sowerby) was present 40 cm above the top of bed 2. *Pinna folium* Young and Bird occurred between 19 cm below the middle of bed 3 and the top of bed 5. *Entolium unare* (Roemer) was present 40 cm above the top of bed 28 of the *paltum* Subzone. *Pleurothamnus costata* (Young and Bird) was found between the top of bed 5 and the boundary between beds 16 and 17. A single occurrence of *Nicelliaria striatata* (Roemer) was found 20 cm below bed 30. Specimens of *Pseudophincta equivalvis* (J. Sowerby) were found between bed 28 of the *paltum* Subzone and 61 cm above the base of bed 19. *Pseudolimnea acuticostata* (Muëller) was present between the base of bed 27 of the *tenusictatum* Subzone and 9 cm below bed 30.

*B. radiata* and *P. dubius* frequently occur as abundant munspecific shell pavements; the two species rarely occur together. Many occurrences of *P. dubius* were found either closely associated with pieces of wood or ammonites, or as stringers (where a ‘stringer’ is defined as a 2D bedding-plane fossil concentration that is very localized and usually elongate with a thickness of less than one shell or other skeletal element (Kidwell et al. 1986)). The stringers of *P. dubius* within the Mulgrave Shale Member are typically 2–5 cm wide and up to 1 m long, and the shells show a degree of clustering around what appear to be common attachment points (Fig. 6). These stringers are found in beds 34–43 but they are particularly common in beds 34 and 35 (Fig. 2).

The three-point moving average of *P. dubius* and *B. radiata* shell abundances in a 20 cm × 20 cm area was calculated and the results are shown in Figure 2. These abundance data and the recorded occurrence of all benthic species (Fig. 2) reveal three very poorly fossiliferous intervals: between 408 and 307 cm below the middle of bed 35; from 223 to 208 cm below the middle of bed 35; and from 40 cm below the middle of bed 35 to 71 cm above the middle of bed 35. At any stratigraphical level within these poorly fossiliferous intervals fewer than four and in most cases no more than one individual of *P. dubius* or *M. substratiata* and no other benthic invertebrate species were found over tens of square metres of exposure (Fig. 2).
Species ranges

The observations presented in this study have altered substantially the biostratigraphical ranges of eight species of marine invertebrates, including six bivalves, a brachiopod and a crinoid. These new ranges are compared with the results of previous work (Table 1; Little 1995; Wignall et al. 2005). Significant changes in range that are outside confidence intervals have been observed for the bivalves *M. substriata*, *B. radiata* and *P . dubius*. The new finds of *P . dubius* and *M. substriata* considerably extend their ranges and also indicate that both these species were present before, during and after the early Toarcian palaeoenvironmental event. *P. dubius* and *M. substriata* therefore did not evolve after extinction horizon 4 of Harries & Little (1999), as suggested by those researchers, but in fact they evolved earlier.

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Zone of the Toarcian. These two species can be clearly distin-
guished from each other. Tate & Blake (1876) did, however, report Goniomya rhombifera (= G. heteropleura of Tate & Blake) in the Lower Sinemurian bucklandi Zone at Redcar, Yorkshire, UK.

The occurrence of the shallow infaunal brachiopod L. longovicensis in beds 48–49 indicates that the environment was suitable for a limited infauna. During this study, no individuals of either Nucinella sp. or the oyster Liostrea hisingeri, as recorded previously by Little (1995), were found. Little (1995) did not record more than two individuals of L. hisingeri at any of the six stratigraphical levels in the Whitby Mudstone Formation, and earlier workers did not record any oysters in the tenucostatum and falciferum zones (Tate & Blake 1876; Hallam 1967).

Very poorly fossiliferous intervals

The bases of the three very sparsely fossiliferous intervals coincide with the abrupt negative carbon isotope shifts ‘A’, ‘C’ and ‘D’ of Kemp et al. (2005) and Cohen et al. (2007) (Fig. 2). The second abrupt carbon isotope shift ‘B’ lies within the first sparsely fossiliferous interval. The duration of the very poorly fossiliferous intervals can be calculated using the astronomical time scale of Kemp (2006). The first poorly fossiliferous interval above negative carbon isotope shift ‘A’ lasted for c. 24 ka, the second above negative carbon isotope shift ‘C’ lasted c. 4000 years and the third above negative carbon isotope shift ‘D’ lasted for c. 11 ka.

Recent Mo-isotope data for samples from the Whitby Mudstone Formation show that each of the carbon isotope shifts ‘A’ to ‘D’ was accompanied by a change in Mo-isotope composition of seawater and Mo abundance (Pearce et al. 2008). Pearce et al. (2008) interpreted these changes to be the result of repeated variations in the areal extent of marine anoxia, which fluctuated broadly in line with precession-driven changes in $\delta^{13}C_{organic}$. It is noteworthy that the variation in the Mo-isotope ratios generally correlate with the changing abundance of *P. dubius* (Fig. 2). Additionally, the concentration of Mo in seawater was exceptionally low during the times of widespread anoxia. It is thus possible that species size and abundance would have been affected not only by the fluctuating levels of seawater oxygenation, but also by the varying availability of Mo, which is an essential bio-essential element (Stiefel 2002).

Palaeoecology of *Pseudomytiloides dubius* and *Bositra radiata*

The inoceramid *P. dubius* is the only benthic taxon present in abundance in the Yorkshire sections when the benthos reappear after the very poorly fossiliferous interval above the first two carbon isotope shifts (‘A’ and ‘B’; Kemp et al. 2005). It continues to be the only abundant species until near the end of the negative carbon isotope excursion and then from the lower falciferum Subzone to the lower commune Subzone. The occurrence of *P. dubius* facies appears to be very closely tied to fluctuations in the areal extent of the oxygen-restricted facies as quantified by the geochemical data of Pearce et al. (2008) and references therein. Observations made during the current study also show that *P. dubius* dominates the assemblage at two stratigraphically lower intervals of the Whitby Mudstone Formation that are organic-rich (beds 2 and 19a; Fig. 3). The posidonid *B. radiata*, on the other hand, occurs only at the beginning and end of the main negative carbon isotope excursion (Fig. 2) and it is absent during the most severe conditions. *B. radiata* and *P. dubius* occur as parautochthonous–autochthonous and autochthonous assemblages, respectively; both species occur as monospecific pavements. Where the two species do coexist, one strongly dominates and the other is rare. The observed distribution is interpreted to be due to the increasing importance of factors such as competitive exclusion, with *P. dubius* having a competitive advantage during periods of lower oxygen levels.

The species ranges and relative changes in the abundance of benthic invertebrates from the early Toarcian sections in Yorkshire, as determined in this study, are notably similar to species distributions and abundance observed in the Dotternhausen, Bisinger Berg, Quarry Kromer and Denkingen sections in SW Germany (Röhl 1998; Röhl et al. 2001; Little 1996). In the falciferum Subzone abundances of *P. dubius* are higher in the Dotternhausen and Denkingen sections (Röhl 1998) but in Germany this subzone is significantly condensed relative to its thickness in Yorkshire. *Bositra radiata* occurs in the semicelatum Subzone in both the Yorkshire and the SW German sections. The new occurrence of *B. radiata* facies reported here above the Top Jet Dogger (Figs 2 and 3) is interpreted to be at a stratigraphically equivalent level to the abundant *Bositra* reported by Röhl (1998) and Röhl et al. (2001) between 30 and 50 cm above the Oberer Stein. In both sections, *Bositra* occurs at the beginning and end of the main negative carbon isotope excursion. It has been previously reported that both *B. radiata* and *B. buchi* occur in SW Germany (Kauffman 1981; Riegraf et al. 1984; Oschmann 1994; Little 1996) but Röhl (1998) and Röhl et al. (2001) considered these to be the single species *B. buchi*.

Jefferies & Minton (1965) suggested that both *B. radiata* and *B. buchi* were nektoplanktonic, having a free swimming ability reminiscent of the valve-clapping action used by the Pectinidae, but this claim is disputed (e.g. Duff 1978; Kauffman 1981; Oschmann 1993; Etter 1996). Oschmann (1993) suggested that *Bositra* may have had a holopelagic possibly progenetic life cycle. Such a scenario is almost impossible to prove owing to the...
lack of any identifying features on the preserved shells. Etter (1996) suggested that a progenetic teleplanic larvae was unlikely for *B. buchi* because of its facies distribution, and spatial and taphonomic patterns. In addition, the observations of this study and others (Jefferies & Minton 1965; Duff 1978; Röhl et al. 2001; Kenig et al. 2004) would indicate that a holoplagic life style is unlikely because *Bositra* is often associated with some infauna, does not occur in the most anoxic facies, and it reaches a fairly large size. Savrda & Bottjer (1987) suggested that the occurrences of *Bositra* within the Toarcian of SW Germany could be interpreted as indicating an environment of prevailing anoxia that periodically underwent re-oxygenation. During re-oxygenation the redox boundary was located at the sediment–water interface allowing colonization by epifaunal but not infaunal organisms. Savrda & Bottjer (1987) termed this occurrence the ‘exaerobic zone’. A further possibility is that *Bositra* had a pseudoplanktonic life habit, but this is highly unlikely because it has not been established convincingly that this species was byssate. Moreover, no association with potential floats has been observed either in this study or previous ones (Kauffman 1981; Wignall & Simms 1990; Oschmann 1993; Röhl et al. 2001). Etter (1996) and Röhl et al. (2001) found relationships between environmental substrate conditions (degree of oxygenation) and the size or abundance of *B. buchi*, which suggests that *B. buchi* was affected by benthic conditions. Most workers thus agree that *Bositra* lived epifaunally and was not byssate (e.g. Duff 1978; Kauffman 1981; Wignall & Simms 1990; Oschmann 1993; Little 1995; Etter 1996; Röhl et al. 2001). *Bositra radiata* probably had a prolonged planktonic larval stage. The observations of this study confirm the suggestions that *B. buchi* and *B. radiata* had a benthic life habit.

It is now generally agreed that *P. dubius* had a benthic life habit and that this species was facultatively pseudoplanktonic (Wignall & Simms 1990; Etter 1996; Little 1996; Röhl et al. 2001). In the Yorkshire sections, the frequent remains of *P. dubius* as stringers (Fig. 6) are interpreted as the remains of bivalves that were attached to material (such as seaweed) that is no longer preserved. These observations are consistent with a facultative pseudoplanktonic life habit for the species and we suggest that its ability to live pseudoplanktonically contributed to its persistence through facies representing hostile marine conditions. It is noteworthy that the stringers of this species are most abundant during the *exaratum* Subzone (Fig. 2) whereas other bivalve species are notably very scarce. The associations of *P. dubius* with potential floating objects are not sufficiently frequent to explain the high abundance of *P. dubius* in the *falciferum* Subzone where it occurs as fairly continuous concordant shell pavements. There are also fairly concordant continuous shell pavements in the *exaratum* Subzone but these are not as frequent as in the *falciferum* Subzone. It seems likely therefore that the populations of *P. dubius* were benthic and had a long-lived planktrophic larval stage (of possibly more than 50 days (Knight & Morris 1996)), and that they were able to establish themselves intermittently during brief periods within the year when conditions on the sea floor became dysoxic rather than anoxic or euxinic.

Comparison of the Toarcian *Bositra* facies and *Pseudomytiloides* facies with the study of the fossiliferous organic-rich mudrocks of the Peterborough Formation (Callovian, Jurassic) by Kenig et al. (2004) provides further insight into the degree of oxygenation during the Toarcian palaeoenvironmental event. Kenig et al. (2004) discussed facies with three different benthic faunal assemblages. They suggested the occurrence of isoreni-atane in all three of these biofacies indicated that recurrent euxinia had extended into the euphotic zone. Kenig et al. (2004) interpreted the faunal assemblages and estimated bivalve life spans to indicate that the different biofacies represent generally euxinic conditions that were punctuated by oxic or dysoxic events of differing duration and extent. The most oxygenated facies in the Peterborough Formation is the weakly bioturbated beds containing abundant *Grphaea*. These are thought to reflect euxinic conditions interrupted by relatively long and better developed periods of oxia or dyoxia (c. 10 years). Facies containing mainly *Melagrinella* and *Bositra*, but also the deposit feeders *Procerithium* and *Mesoacutella*, are interpreted to have been deposited during relatively short oxic or dysoxic periods that interrupted the euxinic conditions. The third and most organic-rich facies of the Peterborough Member (the *Bositra* shale facies) of Bed 10 and the squid bed; Kenig et al. (2004) contains abundant *Bositra*, commonly occurring benthic foraminifers, and sporadic occurrences of benthic gastropods and bivalves such as *Pinna* and *Protocardia*. This biofacies is believed to represent the most extreme euxinic conditions in the Peterborough Formation, where the ‘stratification of the water column with euxinic bottom waters was frequent enough to prevent colonization by true benthic fauna’ and the oxic or dysoxic events were significantly shorter than the *Bositra* with deposit feeders facies. The Toarcian *Bositra* facies between –3.705 m and –2.04 m (Fig. 2) are probably directly comparable with the Callovian ‘*Bositra* shale facies’ as it also contains sporadic *Protocardia* (species 22; Figs 2 and 3). However, *Pinna foliata*, the only *Pinna* species present in the section over this event (species 10; Figs 2 and 3) becomes extinct at the lowest level at which the *Bositra* shell beds occur.

In sharp contrast to the conditions that prevailed during the deposition of the Peterborough Formation, there are three biofacies in the Toarcian of Yorkshire and SW Germany where the low-diversity faunal assemblage and geochemical data indicate three further stages when oxygen restriction was even more extreme. The first of these is the *Bositra* facies between –0.71 m and –2.04 m and from 6.685 to 7.165 m (Fig. 2). This facies is not associated with deposit feeders or other benthic macrofauna, or with any infauna and benthic foraminifers. This facies is likely to represent times where euxinic bottom waters were frequent, with only very short periods of oxic or dysoxic conditions that allowed the planktonic larvae of *Bositra* to settle and briefly colonize. The second facies is the *P. dubius* facies; its pseudoplanktonic life habit, together with a long-lived planktrophic stage, may have allowed it to survive during prolonged euxinic conditions with only brief (perhaps seasonal) periods of oxic or dysoxic conditions. These relatively oxygenated conditions must however have lasted sufficiently long to allow larvae to settle on floating objects such as algae, or on the sea floor, and for populations of *P. dubius* to establish themselves. The most extreme conditions are represented by the very poorly fossiliferous intervals and are directly associated with each of the carbon isotope shifts. The occurrence of only a few individuals of *P. dubius* and *M. substriata* in strata representing many thousands of years indicates highly inhospitable conditions on the sea floor, which must have been almost continuously euxinic. The very low diversity and paucity of macro-invertebrate fauna is fully consistent with biomarker evidence, which indicates that photos zon euxinia was widespread during the *falcigerum* Zone (Schouten et al. 2000; Pancost et al. 2004; Schwark & Frimmel 2004; van Breugel et al. 2006; Fig. 2), with degree of pyritization data (Raiswell et al. 1993) and with the Mo-isotope evidence indicating wide-spread marine anoxia (Pearce et al. 2008).
Bivalve occurrences near the end of the negative carbon isotope excursion

The occurrence of a higher diversity fauna (P. dubius, C. auritus, B. buchi, O. inequivalve and M. substrita) from 65 cm below to 11 cm above the base of bed 39 (the Top Jet Dogger; Figs 2 and 3) indicates that the inhospitable conditions had somewhat ameliorated at this point. This stratigraphical level is interpreted to be the point at which seawater anoxia contracted to regional centres (Pearce et al. 2008); it is also towards the top of the negative carbon-isotope excursion (Fig. 2).

Members of the genus Goniomya are deep infaunal suspension feeders and so the presence of abundant G. rhombifera at the level of the Top Jet Dogger supports the observation of increased species diversity and suggests that the surface sediment had become relatively oxygenated. In the Yorkshire sections, the previous occurrence of deep infaunal bivalve species is before the onset of the negative carbon isotope excursion in bed 31 (stratigraphical level c. –3 m; Figs 2 and 3). Goniomya has also been found at what appears to be an equivalent stratigraphical level at several sections in the SW German Basin (Riegraf 1977; Bandel & Knitter 1986). In addition, Röhl (1998) and Röhl et al. (2001) recorded four bioturbated intervals around the Oberer Stein (equivalent to the Top Jet Dogger) in Dotternhausen, Germany, but did not report any infaunal bivalve species. The distribution of G. rhombifera in the Toarcian sections in Yorkshire is consistent with the evidence of infauna within the contemporaneous strata in Dotternhausen. G. rhombifera has also been found in the bifrons, variabilis, thouarense and levesquei zones in NE Russia (Westermann 1992).

At the top of the faunally diverse interval, numerous (milli-metre-scale) horizons with abundant monospecific B. radiata occur immediately above the faunally diverse interval. These horizons persist for a stratigraphical interval of c. 40 cm (equivalent to a duration of c. 12 ka) after which B. radiata disappears and apparently becomes extinct.

Pattern of extinction

The stepped extinction pattern in the early Toarcian is similar in style to those seen at some other notable extinction intervals (for example, at the Cenomanian–Turonian, Cretaceous–Palaeogene and Eocene–Oligocene boundaries) that have been ascribed to the sampling bias known as the Signor–Lipps effect (Signor & Lipps 1982). Incomplete sampling, taphonomic destruction or the presence of rare taxa causes the artificial random truncation of the stratigraphical ranges of species. Thus species appear to go extinct at some stage before their real extinction and the last observed occurrence of the final taxon precedes the actual extinction time (Signor & Lipps 1982). The oldest point in time at which the true extinction event could have occurred is the last occurrence of the terminal taxon. A compilation of global extinction data (Fig. 4) together with the new high-resolution observations on the macro- and micro-fossils from Yorkshire suggest the following.

(1) There is a maximum of three extinction horizons that are here denoted as extinction horizons i, ii and iii (Figs 2, 3 and 4). However, it may be that there is only one, or possibly two, true extinction horizons (extinction horizons iii, or i and iii) and that the others are artefacts of the Signor–Lipps effect. In this case, extinction horizon ii and possibly extinction horizon i are apparent extinctions. This possibility is discussed further below.

(2) Apparent extinction horizon i lies just above the Pliensbachian–Toarcian boundary, within the palatum Subzone, near the top of bed 1 (Fig. 3). This horizon is equivalent to the regional extinction step (2) of Harries & Little (1999, fig. 4) (see Fig. 3) and to the Pliensbachian–Toarcian boundary extinction of Wignall & Bond (2008). It is likely that the extinction ‘event’ is taken at the stage boundary in several sections elsewhere as a result of stratal gaps and/or low-resolution biostratigraphical control.

(3) Apparent extinction horizon ii is placed near the middle of the semicelatum Subzone (sensu Subboreal zonation). It is equivalent to the regional extinction step (3) of Harries & Little (1999) and approximately to the mid-semicelatum extinction of Wignall et al. (2005). The data from the Cleveland Basin suggest that the highest percentage of macrofossil extinctions occur at this horizon (Fig. 3); the horizon also corresponds to a local faacies change.

(4) Extinction horizon iii, based upon the stratigraphically complete section in the Cleveland Basin, is placed near the top of the semicelatum Subzone. This extinction horizon is particularly well marked by ostracode extinctions, a decrease in the relative abundance of calcareous nannofossils and dinoflagellates, and several dinoflagellate extinctions (Prauss et al. 1991; Boomer 1992; Boomer & Whatley 1992; Nikiènko & Shurygin 1992; Palliani et al. 2002; Tremolada et al. 2005; Zakharov et al. 2006). The small size of these fossils gives rise to more continuous preservation potential (Raup 1989) and does not present the same sampling bias problems that macrofossils do.

(5) The regional extinction step (1) of Harries & Little (1999) involves only a few species and is not supported by data from other sections around the world. We propose that this extinction is most likely to reflect local faacies changes and sampling bias and that it is part of one of the later extinction events.

(6) Wignall et al. (2005) suggested that benthic extinctions preceded pelagic extinctions in southern Europe, with the majority of benthic extinctions occurring at the Pliensbachian–Toarcian boundary and the majority of pelagic extinctions occurring at the semicelatum Subzone extinction event (as defined by those workers). Wignall et al. (2005) believed that the opposite pattern occurred in NW Europe. However, no evidence has been found in this study to substantiate this interpretation. In fact, most taxonomic groups, whether pelagic or benthic, appear to undergo substantial extinctions in roughly equal proportions at both extinction horizons i and iii (Fig. 4).

Taking the Signor–Lipps effect into account, the two most likely scenarios for the early Toarcian extinction horizons are as follows. (1) There is only one true extinction horizon and the oldest point in time at which this could have occurred is at extinction horizon iii (upper semicelatum Subzone). In this scenario the two preceding extinction horizons (i and ii) are artefacts of the Signor–Lipps effect. This interpretation is strongly supported by positions of the microfossil extinctions and by changes in relative abundances. (2) There are two true extinction levels: an older event just above the Pliensbachian–Toarcian boundary (i.e. extinction horizon i) and a second event in the upper semicelatum Subzone (i.e. extinction horizon iii).

The possible existence of a separate extinction horizon i is supported by the observations that it coincides with significant change in the 87Sr/86Sr of seawater (McArthur et al. 2000), which was probably related to the onset of the eruption of the Karoo–Ferrar Large Igneous Province (Cohen et al. 2004, 2007), and with an earlier negative carbon isotope excursion close to the Pliensbachian–Toarcian boundary (Hesselbo et al. 2007; S.P. Hesselbo, pers. comm.). Correlation of the biotic changes identified in this study with the carbon isotope data of Kemp et al. (2005) shows that apparent extinction horizon ii corresponds
to the start of the long-term negative carbon isotope excursion (Fig. 2). This correlation differs from that of Wignall et al. (2005), who suggested that the mid-semicelatum Subzone extinction did not coincide with, but preceded, the negative carbon isotope excursions in Yorkshire.

Extinction horizon iii corresponds to the first abrupt carbon isotope shift ‘A’ as defined by Kemp et al. (2005). This isotope shift marks the first of the four abrupt shifts that constitute the major steps in the early Toarcian negative carbon isotope excursion. The extinction also corresponds to the onset of a large shift in the Os-isotope composition of seawater (Cohen et al. 2004) and to an increase in the rate of increase of 87Sr/86Sr of seawater (McArthur et al. 2000), interpreted to indicate accelerated rates of global weathering (Cohen et al. 2004). There is also a marked change in the Mg/Ca and δ18O composition of belemnites, which suggests that sea surface temperatures increased by c. 7–13 °C (McArthur et al. 2000; Bailey et al. 2003). Furthermore, extinction horizon iii occurs at exactly the same stratigraphical level as Mo-isotope data provide evidence for a significant increase in the areal extent of sea-water anoxia (Pearce et al. 2008). There is thus abundant independent geochemical evidence that, when taken together, argues for major changes in global environmental conditions at extinction horizon iii.

Conclusions

(1) A compilation of worldwide macro- and micro-fossil data, together with new high-resolution macro-fossil data from the Cleveland Basin, has allowed us to recognize three extinction horizons in the Early Toarcian. These horizons are in the paltum Subzone (extinction horizon i), the mid-semicelatum Subzone, sensu Subboreal Province (extinction horizon ii), and the upper semicelatum Subzone (extinction horizon iii). Taking into account the Signor–Lipps effect, it is possible that only one true extinction occurred (extinction horizon iii), in the upper semicelatum Subzone.

(2) Extinction horizon iii is synchronous with changes in environmental proxies that indicate an increased rate of chemical weathering (Cohen et al. 2004), a major change in the global carbon cycle (Hesselbo et al. 2000; Kemp et al. 2005) and a large increase in seawater temperature (McArthur et al. 2000; Bailey et al. 2003). Mo-isotope data indicate that seawater anoxia became much more widespread at this time (Pearce et al. 2008).

(3) P. dubius dominates the succession over the main part of the carbon isotope excursion when the conditions were highly inhospitable. It is very tolerant of and even seems to have a high tolerance for anoxia became much more widespread at this time (Pearce et al. 2008).

(4) Abundance data for all species from the Yorkshire sections, including the most tolerant or well-adapted species P. dubius, show that there was an almost complete absence of fossils within three notable intervals, which are interpreted to represent the most inhospitable conditions. The base of these intervals corresponds to negative carbon isotope shifts ‘A’, ‘C’ and ‘D’ of Kemp et al. (2005) and Cohen et al. (2007). The first very poorly fossiliferous interval also encompasses the second abrupt carbon isotope shift ‘B’.

(5) The species M. substriata, P. dubius and B. radiata all survived the environmental crisis that is defined by the negative carbon isotope excursion of the exaratum Subzone. Thus, seven species survived the palaeoenvironmental crisis, rather than four as thought previously. Although G. rhombifera was not present for some time before the event, this species also survived the event.

(6) B. radiata became extinct close to the base of the falciferum Subzone near the end of the negative carbon isotope excursion.

(7) B. radiata is found only immediately before carbon isotope shift ‘A’ when conditions were beginning to deteriorate and at the end of the overall negative carbon isotope excursion when conditions were beginning to improve. We suggest that these limited occurrences were likely to have been related to its inability to survive the conditions that prevailed throughout the main period of the negative carbon isotope excursion and its preference for suboxic or dysoxic conditions.

(8) The increased diversity of epifaunal bivalve species and the occurrence of the deep infaunal bivalve G. rhombifera indicate that conditions became relatively oxygenated near the end of the negative carbon isotope excursion. Our observation is the first finding of this species in the Whitby Mudstone Formation, and its presence here is consistent with its occurrence in the SW German Basin. This period of relatively high oxygenation appears to have been contemporaneous in both basins and perhaps further afield as well.

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