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The impact of anoxia on pelagic macrofauna during the Toarcian Oceanic Anoxic Event (Early Jurassic)

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ABSTRACT

Extreme environmental change during the Toarcian Oceanic Anoxic Event had widespread impacts on marine biota. This study provides new evidence, from the Yorkshire coast sections, UK, that the event was associated with periods of elevated fish and ammonite mortality. Using a synthesis of pelagic macrofaunal changes, benthic macrofaunal data and geochemical proxies we show that there are stratigraphical correlations between: (1) pelagic macrofaunal ranges and abundance, (2) benthic macrofaunal abundance, and (3) geochemical proxies that indicate deoxygenation. We identify eight stratigraphical intervals of differing character. Results suggest two major phases of relatively persistent deoxygenation with photic zone euxinia. The cyclostratigraphic timescale indicates that each phase lasted at least tens of thousands of years. Belemnite migration during the event probably resulted from increased seawater temperatures and low food supply similar to that observed for many marine taxa, including squid, within the present-day oceans.

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1. Introduction

The early Toarcian Oceanic Anoxic Event (OAE) was a period of sudden and severe global palaeoenvironmental change characterized by enhanced global burial of organic carbon (Jenkyns, 1988, 2003; Fig. 1a). This OAE is associated with a mass extinction of marine organisms (e.g. Benton, 1995; Little, 1996; Aberhan and Fürsich, 1996; for global summary see Caswell et al., 2009) and a large eustatic sea-level rise (Hesselbo and Jenkyns, 1998). Geochemical proxies provide evidence for the following palaeoenvironmental changes: increased seawater surface temperature by up to 7–13 °C (Bailey et al., 2003; Suan et al., 2008), elevated levels of continental weathering (Cohen et al., 2004), substantial perturbations to oceanic and atmospheric carbon cycles (e.g. Hesselbo et al., 2000; Röhl et al., 2001; Kemp et al., 2005; Hesselbo et al., 2007; Hermoso et al., 2009; Al-Suwaidi et al., 2010; Hesselbo and Pienkowski, 2011), a global increase in the areal extent of marine reducing conditions (Pearce et al., 2008), and a euxinic (contains H₂S) water column (Schwark and Frimmel, 2004). Cyclostratigraphical analysis of the Yorkshire sections (Kemp et al., 2005, 2011)

indicates one regular astronomical cycle of 75 cm throughout the record of the OAE preserved on the Yorkshire coast and therefore that sedimentation rate was constant at this scale and in this area over the interval studied. Most of the high-resolution integrated studies of the Toarcian OAE have used the sections along the Yorkshire coast. These sections represent part of the Cleveland Basin succession (Fig. 1a–c).

1.1. Toarcian pelagic faunal changes

Caswell et al. (2009) reviewed the macrofauna and microfossil data supporting the four extinction levels proposed for the late Pliensbachian – early Toarcian interval by Harries and Little (1999) and argue that during the early Toarcian there was one definite marine extinction horizon near the top of the *Dactyloceras* (*Orthodactylites*) *semicelatum* Subzone (horizon iii, Fig. 2). There is also evidence for a second global extinction horizon near the Pliensbachian–Toarcian boundary (horizon i, Fig. 2). Horizon i is less certain, because whilst a significant number of species disappeared near Pliensbachian–Toarcian boundary, it could be a function of the Signor-Lipps effect related to the *semicelatum* Subzone extinction (horizon iii), and/or poor biostratigraphical control and/or environmental changes (Caswell et al., 2009). Contemporaneous carbon isotope data provide support for at least regional scale environmental change (Hesselbo et al., 2007;

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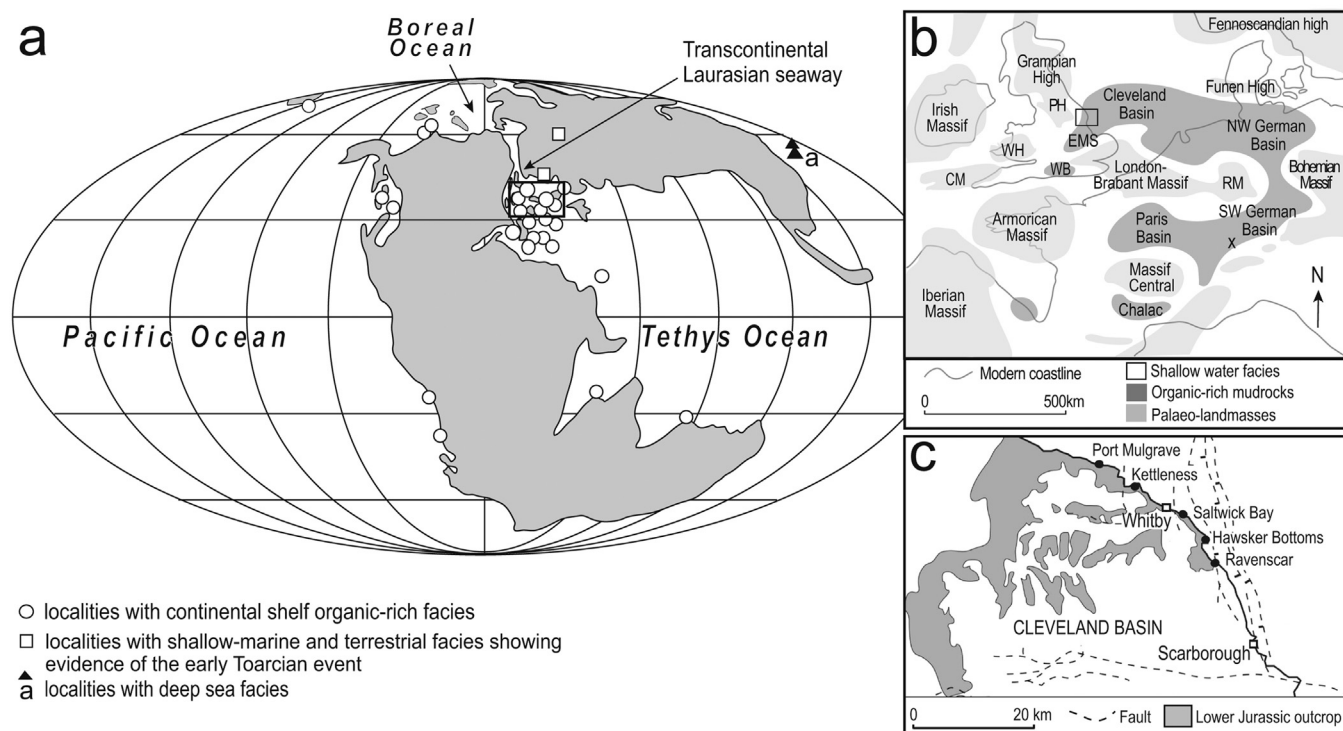


Fig. 1. Palaeogeographical maps for the early Toarcian modified from Caswell et al. (2009). (a) Global palaeogeographical map showing the distribution of the continents, position of the oceans and location of the key sections with different facies. Inset box shows area of covered by (b). (b) European palaeogeography showing the widespread distribution of organic-rich facies and the present-day coastline. Inset box shows area covered by (c); x = location of the Dottershausen section; PH = Pennine High; WH = Welsh High; CM = Cornubian Massif; EMS = East Midlands Shelf; WB = Wessex Basin; and RM = Rhenish Massif. (c) Map of the Cleveland Basin showing the Lower Jurassic outcrops and study sites along the Yorkshire coast.

Littler et al., 2010). The extinction pattern in the Cleveland Basin was more severe for benthic fauna (Little, 1996) and detailed studies of this basin have focused on the benthos (e.g. Little, 1996; Aberhan and Fürsich, 1996; Röhl et al., 2001; Caswell et al., 2009). However, the pelagic macrofauna across NW European and in Tethyan areas were also affected (e.g. Cecca and Macchioni, 2004; Dera et al., 2011). In NW Europe the early Toarcian nekton was dominated by ammonites, belemnites and large marine reptiles that predated upon them including crocodiles, ichthyosaurs and plesiosaurs (Benton and Taylor, 1984). The marine reptile fauna in Yorkshire and Germany were similar, but with relatively more ichthyosaurs and fewer crocodiles and plesiosaurs in SW Germany (Benton and Taylor, 1984).

Near the Pliensbachian–Toarcian boundary (extinction horizon ii; Fig. 2) endemic ammonite species became extinct in both Boreal and Mediterranean realms (Cecca and Macchioni, 2004), when Tethyan (e.g. *Protogrammoceras*) and pandemic (e.g. *Dactylioceratidae*) species migrated into NW Europe ending Tethyan–Boreal provinciality. Significant global extinctions occurred within ammonite faunas of both Tethyan and Boreal areas near the top of the *semicelatum* Subzone (extinction horizon iii; Caswell et al., 2009). *Pleuroceras hawskerense* became extinct and with this the Boreal family Amaltheidae was lost (Little, 1996; Cecca and Macchioni, 2004). Additionally, at this time species from three ammonite suborders (Ammonitina, Phylloceratina and Lytoceratina) underwent global extinctions (Cecca and Macchioni, 2004). Diversification following extinction horizon (iii) was rapid, and the fauna was totally renewed within the *Harpoceras falciferum* Subzone (Little, 1996; Cecca and Macchioni, 2004). Dera et al. (2011) suggested that the geographical range expansions/displacements of ammonites were driven by palaeoclimatic changes, such as sea surface temperature which, in turn, drove a rise in eustatic sea-level increasing the connections and thus faunal

exchange between the basins, and that the success of the ammonite invasions was facilitated by extinction of endemics. The ecology of ammonites is uncertain because there are no appropriate analogues but, being a highly diverse taxon, life habit probably varied inter-specifically and throughout ontogeny. Westerman (1996) concluded that most ammonites lived pelagically (swimmers, drifters or vertical migrants) but that others were demersal. Ammonite morphology suggests that nektonic species were significantly slower swimmers than belemnites (Westerman, 1996).

True belemnites first appeared in Europe during the Hettangian, and in the Toarcian widespread dispersal outside of Europe occurred, and species diversity and origination reached a maximum (Doyle, 1987). During the Middle Jurassic distinct biogeographic provinces developed and belemnites migrated between them several times (Doyle, 1987). Belemnites are extinct and interpretation of life habit is based on modern analogues (cuttlefish and pelagic teuthid squid); these are fast swimmers with varied behaviour, migrating vertically within the water column, and between regions on various temporal scales (Rexfort and Mutterlose, 2009). Therefore belemnite life habit probably also varied substantially between species.

1.2. Deoxygenation and aims of this study

By measuring the Mo-isotope composition ($\delta^{98/95}\text{Mo}$), Re/Mo ratios and Mo concentration of samples from the Yorkshire succession (Fig. 2) Pearce et al. (2008) postulated that there were four periods during the Toarcian OAE when the areal extent of deoxygenation increased globally. This interpretation is based on the observations that (i) the proportion of the oceans with particular redox characteristics influences the isotopic composition of Mo ($\delta^{98/95}\text{Mo}$) in seawater (Siebert et al., 2003; Pearce et al., 2008). $\delta^{98/95}\text{Mo}$ Mo

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