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Recovery of benthic communities following the Toarcian oceanic anoxic event in the Cleveland Basin, UK

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Abstract

During the Toarcian oceanic anoxic event (OAE) considerable environmental changes occurred that were associated with global warming, perturbations to the C-cycle and ocean deoxygenation which resulted in a mass extinction of marine fauna. Recovery of the biota after the event was protracted and has to date undergone limited study. However, understanding the patterns and processes of recovery are critical to anticipating ecosystem responses to the environmental changes predicted for the near future. Results showed that increases in benthic diversity, and the re-establishment of the Toarcian infauna was gradual and followed the changing redox conditions. Pioneering infauna, such as *Dacryomya ovum* that dominated the

seafloor after the event in the Cleveland Basin, Yorkshire, UK, can modify the physico-chemical environment and thus facilitate ecological succession after disturbance. The length of *D. ovum* increased >8 mm throughout the *bifrons* Zone and these body-size changes were linked with total organic carbon (TOC) content suggesting a link to primary productivity, although only at intermediate levels of deoxygenation. Major changes in the phytoplankton, and so food supply, seem to have driven changes in bivalve body size, across trophic guilds, both during and after the event in Yorkshire, and on the mid to lower shelf in Spain and France, respectively. Primary productivity collapse seems then to have been a major driver of biotic change throughout the Toarcian event, as it was during the Permian–Triassic, Triassic/Jurassic and Cretaceous/Tertiary mass extinctions. Further investigation of both the palaeontological and geochemical changes that occurred within early successional Toarcian infaunal communities are required to more fully understand the pattern of recovery after the OAE.

Keywords: Jurassic; Lilliput effect; shell morphology; population structure; dysoxia; Alum Shale Member

1. Introduction

In early Toarcian (~183 Ma) global warming occurred, recorded as a 7–13°C increase surface ocean temperatures (Bailey et al. 2003; Gomez and Arias 2010; Korte et al. 2015; Suan et al. 2008) which was associated with increases in atmospheric $p\text{CO}_2$. Large negative carbon isotope excursions are recorded in marine organic matter, marine carbonates, fossil plants and wood across the northern (Caruthers et al. 2011; Kemp et al. 2005; Hermoso et al. 2009a, Hesselbo et al. 2007, Hesselbo and Pienkowski 2011, Röhl et al. 2001; Ullmann et al. 2014) and southern hemispheres (Al-Suwaidi et al. 2010; Gröcke et al. 2011; Kemp and Izumi 2014). The warming

was accompanied by sea level rise (Haq, 2017; Hesselbo and Jenkyns 1998), increased rates of continental weathering (Cohen et al. 2004) and changes in the patterns of ocean primary productivity (Jenkyns 2010) which triggered an oceanic anoxic event (OAE).

Contemporaneous global ocean deoxygenation (N. B. encompassing both hypoxia (1-30% of saturation) and anoxia (absence of oxygen)) is indicated by the enhanced widespread deposition of marine organic carbon (Jenkyns 1988), and changes in proxies for seawater redox (Pearce et al. 2008; Thibault et al. 2018) although the extent of the deoxygenation varied geographically (Hermoso et al. 2009b; Kemp and Izumi 2014; Rodriguez-Tovar and Reolid 2014). Early Toarcian ocean deoxygenation is linked with a mass extinction of marine life (Caswell et al. 2009; Little and Benton 1995, Little 1996), biogeographic range shifts of key taxa (Caswell and Coe 2014; Dera et al. 2011; Nikitenko et al. 2008), and large shifts in seafloor community composition (Caswell and Frid 2017; Danise et al. 2013; Danise et al. 2015) and the body size of taxa that dominated the seafloor during the OAE (Caswell and Coe 2013). Large decreases in the amount of dissolved oxygen in the oceans have occurred over the last 60 years as a consequence of global warming and anthropogenic nutrient inputs (Diaz and Rosenberg 2008; Stramma et al. 2010); and models predict a continued decline of up to 7% over the next century (Keeling et al. 2010). The ecological changes that occurred during the Toarcian are commensurate with the mass mortalities (Breitburg et al. 2018; Falkowski et al. 1980), changes in organism behaviour (Gray et al. 2002; Riedel et al., 2014; Seitz et al. 2003), growth rates and body size (Caswell and Coe 2013; Cheung et al. 2013) that are occurring in deoxygenated areas today.

During the early Toarcian the seafloor in NW Europe was dominated by the epifaunal suspension feeding bivalves *Bositra radiata* and *Pseudomytiloides dubius*

before and during the OAE (*Dactylioceras tenuicostatum* and *Harpoceras exaratum* ammonite subzones), respectively, which underwent large shifts in abundance and body size during the event (Caswell et al. 2009, Röhl et al. 2001). Changes in the size of these species have been linked to changes in primary production (Caswell and Coe 2013). Although we now know how some Toarcian marine communities changed during the event (Caswell and Coe 2013; Clemence et al. 2015; Danise et al. 2013; Fürsich et al. 2001; Gomez and Arias 2010; Röhl et al. 2001), we know comparatively little about the faunal changes that occurred during the recovery from the OAE (which is geochemically defined as the *exaratum* Subzone; Pearce et al. 2008). The present study considers changes in the benthic communities, of the Cleveland Basin, Yorkshire, UK, in the aftermath of the OAE (*Dactylioceras bifrons* ammonite Zone). The benthos remained impoverished for a considerable period, requiring >900 kyr for the infauna to return (Caswell and Frid 2017), despite the somewhat improved conditions, as indicated by a suite of geochemical proxies (Cohen et al. 2004; Hesselbo et al. 2000; Kemp et al. 2005; Kemp et al. 2011; Pearce et al. 2008; Raiswell et al. 1993).

The post-OAE seafloor communities were of low diversity and were dominated by the nuculanid bivalve *Dacryomya ovum* (Sowerby) in the *bifrons* Zone. This was the first infaunal taxon to occur in abundance after the OAE in the Cleveland Basin, i.e. specimens of the infaunal brachiopod *Lingula longovicensis* and the bivalve *Goniomya rhombifera* occur briefly (at the top of Beds 38 and 48, respectively; bed numbering after Howarth 1962; Caswell et al. 2009) but are not abundant. *D. ovum* occurs abundantly in the UK within Toarcian organic-rich mudrocks (Hesselbo and Jenkyns 1995; Horton and Edmonds 1987; Little 1996; Martin 2004; Morris 1979; Watson 1982). Nuculanids with strong taxonomic affinities to *D. ovum* occur in coeval organic-rich strata worldwide, including: *Dacryomya*

lacrymya in the Toarcian Schistes Cartons, France (Fürsich et al. 2001), *Nuculana* (*Praesaccella*) *ovum* in Sinemurian–Toarcian facies in Spain (Gahr 2002), Chile, Argentina (Aberhan 2002; Damborenea 1987) and British Columbia (Aberhan 1998). *Dacryomya* spp. Also occurred in Toarcian successions in Russia and Siberia (Nikitenko and Shurygin 1992; Shurygin 1983; Zakharov et al. 2006).

Organism body-size affects fundamental physiological, ecological and evolutionary processes. For example, organism life history, metabolic rates, the geographic range and extinction rates of organisms all scale disproportionately with body mass (Smith and Lyons 2013). Notable decreases in body-size have been recognised after at least six extinctions (Girard and Renaud 1996, Gobbett 1973; Harries 1993; Håkansson and Thomsen 1999; Kaljo 1996, Ward et al. 2004) including the early Toarcian (Caswell and Coe 2013, Voros 2002) when organisms of small, or stunted, size dominate which is thought to be a phenotypic reaction to unfavourable growth conditions (known as the ‘Lilliput effect’; Urbanek 1993).

Bivalve intraspecific shell morphology has also been shown to vary with deoxygenation. For instance, in the Baltic Sea the normally suborbicular shells of *M. balthica* become elongated with a flexed posterior end which correlates with increasing hypoxia, and has been linked with siphon extension above the redox boundary (Sokołowski et al. 2008). Fossil *D. ovum* have a similar elongated (or ‘rostrate’) posterior and we hypothesise that variations in the degree of elongation could have helped *D. ovum* to colonise the seafloor after the Toarcian OAE.

Infaunal taxa, such as *D. ovum*, can act as ecosystem engineers (Jones et al. 1994) in that they alter the physicochemical environment by burrowing: their bio-irrigation of the sediment increases oxygenation, redistributes sediment particles,

organic material, minerals and microbes; in the process sedimentary structures and biogeochemical gradients are created (Welsh 2003). Sediment mixing increases the habitable area available to taxa that are intolerant of low oxygen (Meysman et al. 2006); and, the creation of biogeochemical gradients affects the sedimentary fluxes of nutrients in to the water column stimulating primary productivity (Graf and Rosenberg 1997; Jørgensen et al. 1995; Kristensen 2000). The increased sediment heterogeneity and habitat complexity stimulates biodiversity. So, the appearance of infaunal bivalve populations after the OAE would have been an important step in the recovery of the seafloor communities.

This study aims to determine the patterns of change within the benthic communities of the *bifrons* ammonite Zone during the recovery from the Toarcian OAE. The development of early successional benthic communities dominated by *D. ovum* (usually monospecific) were investigated in terms of their taphonomy, palaeoecology, morphometry and life history from sections near Whitby, North East Yorkshire, UK. Changes in Yorkshire are considered for both *D. ovum* populations and the whole benthic macrofaunal community.

2. Methods

2.1 Geological setting

The lower Jurassic succession was deposited in the Cleveland Basin, Yorkshire, UK that extends into the Sole Pit Trough of the North Sea Basin (Fig. 1). The 71 m thick lower Toarcian Whitby Mudstone Formation was deposited in a semi-restricted fully marine basin below storm wave base, and the lithology is typical of the organic-rich mudrocks that were deposited across NW Europe at that time (Jenkyns 1988, Jenkyns 2010, Hesselbo and Jenkyns 1995). It is one of the most complete and expanded exposures of the Late Pliensbachian – Early Toarcian period in the world (and includes the Global Boundary Stratotype Section and Point for the base of the

Pliensbachian Stage). The formation is biostratigraphically subdivided into five ammonite zones described in detail by Howarth (1955, 1962, 1973, 1992).

2.2 Field data collection

Populations of the bivalve *Dacryomya ovum* (Sowerby) were sampled throughout the organic-rich facies of the Whitby Mudstone Formation between Whitby (54°29'28.48"N, 0°36'33.89"W) and Saltwick Bay (54°31'15.84"N, 0°35'15.68"W), NE Yorkshire, UK (Figs 1, 2A–H). Approximately 30 m of vertical section, from the upper 3 m of the Mulgrave Shale Member to the lower 27 m of the Alum Shale Member (upper *Harpoceras falciferum* to *Catacoeloceras crassum* ammonite subzones; Fig. 3), were sampled from bedding planes in the foreshore exposures and sea cliffs. Benthic macrofossil presence and absence data were collected approximately every 0.5m. Data and samples for morphometric analyses were collected from 30 discrete levels throughout the range of *D. ovum* (where it occurred in abundance). Each observation/sample was precisely located relative to known stratigraphic datums based on Howarth (1962).

At each of the 30 stratigraphic levels the following information was recorded: *D. ovum* abundance, the shell orientation within the bedding (e.g. parallel, orthogonal or oblique), and the compass orientation of the posterior end relative to the azimuth. At each level all fossils were marked and bedding planes were photographed at high resolution for spatial analyses of shell clustering. Subsequently, all body fossils were extracted from each level for later measurement in the laboratory. The spatial clustering of shells within each bedding plane was determined from field photographs using the nearest neighbour statistic, R , from the method of Hammer and Harper (2006) where $R = \frac{d}{0.5 \times (\frac{a}{n})}$ and d is the mean distance of each object from its nearest neighbour, a is the total area surveyed, and n is the total number of objects. Clustering was indicated by $R \leq 1.00$ and dispersal by $R \geq 1.01$.

2.3 Shell morphometrics and growth

Shell height, length and inflation were measured (Fig. 2A and 2H) for all extracted body fossils ($n = 629$) to the nearest 0.01 mm using digital Vernier callipers. The shell height and length of external moulds ($n = 206$) were measured in the field. For the small number of disarticulated specimens ($n = 15$), shell inflation was measured from a single valve and doubled. Ratios of shell height: shell inflation were calculated, for all extracted fossils, to provide an index of the degree of *post mortem* lateral shell compaction (e.g. Fig. 2F–G). Population size structure was explored using the length frequency distributions (LFDs).

To investigate variations in shell shape between the different assemblages high-resolution photographs were taken of the exteriors of all extracted right valves (complete fossils and internal moulds; $n = 633$). For the disarticulated specimens (2% of shells collected) both the left and right valves were measured. Fifteen measurements were made (Fig. 2A) from each fossil using the measure and angle tools (the latter to delineate the 14 dorso-ventral measurements) in Image J (version 1.49m, NIH) on calibrated photographs and three indices to describe shell shape (derived by Sokolowski *et al.* 2008) were calculated, as follows.

$$SDI1 = \frac{((UV + US)) / 2}{(UE + UF + UG + UH + UI) / 5} \quad (1)$$

$$SDI2 = \frac{(UJ + UK) / 2}{(UE + UF + UG + UH + UI) / 5} \quad (2)$$

$$SDI3 = \frac{UV + US}{UJ + UK} \quad (3)$$

SDI1 describes the flexure of the posterior shell margin (low values indicate high flexure), and SDI2 compares the symmetry of the posterior and anterior shell margins (low values indicate greater asymmetry). SDI3 describes the differences in shell elongation between the posterior and anterior end (low values indicate greater elongation of the posterior).

External growth rings were counted for six complete valves of *D. ovum* (from four assemblages) and the distances between them were measured along the axis of maximum growth. Annuli were identified on the basis of their morphological distinctiveness (boldness, colour, topography and continuity across the shell surface) when examined under a light source. Using the shell height at age data and the software Fishparm v.3 (Prager et al. 1994) shell growth was modelled using the von Bertalanffy growth function $H_t = H_{\infty} (1 - e^{-k(t-t_0)})$ (Jones et al. 1989; von Bertalanffy 1938). Where, t = age (years), H_t = shell height at age t , H_{∞} = maximum shell height, K = growth constant and t_0 = age when $H = 0$. Using the growth constant, an omega value (ω), indicative of population growth rate, was derived from $\omega = kH_{\infty}$ (Carroll et al. 2011).

2.4 Data analysis

Changes within the *D. ovum* assemblages are considered within the context of the whole benthic community using data on body fossil occurrences from Little (1995, 1996) and Caswell et al. (2009), and data on trace fossils from Martin (2004). The relationships between biotic variables were explored using reduced major axis linear regression using Past.exe (Hammer and Harper 2001, 2006). The relationships between shell morphometrics and palaeoenvironmental changes were explored using stepwise multiple regression (SPSS v. 21) with geochemical proxy

data for primary production (TOC; from Cohen et al. 2004 and Harding 2004), palaeoredox ([Mo], [U], TOC/TS; from Harding, 2004, Pearce et al. 2008 and McArthur et al. 2008) and surface seawater temperature ($\delta^{18}\text{O}_{\text{belemnite}}$; from McArthur et al. 2008 and Ullman et al. 2014; proxy data for benthic water temperatures being unavailable). The multiple regressions were performed on the complete data and subsets of the data subdivided based on the median TOC content (2%). Using subsets of the data allowed us to account for changes in the response of environmental drivers under different redox conditions. The differences between biotic parameters were explored between the different assemblages and the two categories ($\leq 2\%$ and $\geq 2\%$) of TOC using nonparametric tests such as the Kruskal-Wallis, Jonckheere-Terpstra and Mann Whitney U-test (using SPSS v. 21).

Fossil preservation varied stratigraphically: in assemblages below 49.4m almost all fossils were preserved as complete body fossils and above 49.4m they were preserved as internal moulds (Supplementary Table S1). To explore changes in body size and shape through time these data had to be pooled. The measurements for fossils preserved as internal moulds might be expected to underestimate the actual body-size due to the lack of a shell. Therefore interpretations of the size differences between assemblages comprised entirely of body fossils (with shell) and those comprising internal moulds underestimate the true size difference between these stratigraphic levels by ~3 mm (the measured shell thickness).

3. Results

3.1 Taphonomy of *Dacryomya ovum* assemblages

Within the Alum Shale Member *D. ovum* occurs in matrix supported shell pavements. Most occurrences were monospecific except for pyritised trace fossils that were present at some levels (Fig. 4). Most *D. ovum* were preserved as complete

body fossils (54%), a further 30% were preserved as internal moulds and 16% as external moulds. Only 2% of shells were disarticulated into their separate valves. Although 20% of fossils showed some fractures (Supplementary Information Table S1; Fig. 2) the majority were undamaged. *D. ovum* preservation varied through time: between 38.00 and 49.35 m most shells were preserved as body fossils, and above 49.47 m most were preserved as internal moulds (Supplementary Information Table S1). This suggests that the factors influencing preservation changed in the lower *Peronoceras fibulatum* Subzone.

The body fossils were comprised of shell material, most were filled with the mudrock matrix and some had a thin layer of pyrite coating the inner shell surface. One specimen from 51.22 m had the inarticulate brachiopod *Discinisca infraoolithica* attached to the outer surface, but there was no evidence for boring or other epibiont overgrowth. The nature of the shell pavements and the lack of disturbance (e.g. disarticulation, shell breakage, and epibiont overgrowth) suggest the *D. ovum* pavements are autochthonous or parautochthonous assemblages representing biogenic concentrations of fossils in near-life position.

3.1.1 Shell compaction

Un-compacted *D. ovum* shells are naturally inflated with a rostrate posterior end (which is typical of the genus; Table 3, Fig. 2A-B) the extent of which varied between individuals (Fig. 2B-E). Most inflated *D. ovum* specimens without visible signs of compaction had shell height/inflation (h/i) ratios between 1.1 and 1.3 (Fig. 2B-E), shells with some evidence of compaction (e.g. shell fractures and collapsed areas) had ratios of 1.4–2.73 (Fig. 2F-G), and shells which appeared highly compacted had ratios >2.73. Of all specimens measured 20% were uncompacted, 50% were moderately compacted and the remaining 30% were significantly

compacted. Shell height/inflation was not correlated with shell length, height, nor the three shape ratios (reduced major axis linear regression $p > 0.05$). Thus, the lateral compaction of shells, as indicated by shell height/shell inflation, does not seem to have influenced these morphometric parameters. Examination of the specimens showed that one valve was usually inflated whereas the other collapsed and fractured under compression (Fig. 2F). *D. ovum* shell height/inflation decreased throughout the section (Fig. 3A; linear regression, $R^2 = 0.52$, $F = 29.73$, $p < 0.001$) meaning shells were more compacted in the lower part of the section.

3.1.2 Spatial distribution of fossils within shell pavements

Shells were concordant (e.g. parallel), oblique and perpendicular to the bedding. However, in most *D. ovum* assemblages (67%) shells were concordant. At five stratigraphic levels $\geq 50\%$ of fossils were oblique or perpendicular to the bedding. These shells were considered to be in an infaunal life position within the sediment, and so represented an autochthonous assemblage. Bivalve shells that have rostrate posterior ends, like *D. ovum*, tend to live with the long-axis oriented vertically with the posterior projected towards the sediment surface (Stanley 1970, Stanley 1981). Shells that were concordant with the bedding may be parautochthonous or may reflect differences in living habit between assemblages due to environmental changes.

Nearest neighbour analyses showed that in 12 of the shell pavements shells were clustered ($R = 0.32$ to 0.98) within the bedding plane, and in the other 17 they were dispersed ($R = 1.02$ to 2.86 ; Fig. 4), and there was no trend through time (linear regression $R^2 = 0.025$, $F = 0.73$, $p = 0.40$). At most stratigraphic levels *D. ovum* shells had bimodal or multimodal compass orientations with a prevailing north-northeast to south-southwest flow axis (mean $197^\circ \pm 4^\circ$) throughout the upper half of the *bifrons* Zone (Supplementary Information Fig. S1).

3.2 Shell size and shape of *Dacryomya ovum*

Dacryomya ovum mean shell size fluctuated approximately two fold throughout its stratigraphic range, up to 10 mm shell length and 4.5 mm shell height (Fig. 4). Median shell length (Kruskal Wallis, $X^2 = 231.6$, $p < 0.001$), height (Kruskal Wallis, $X^2 = 109.8$, $p < 0.001$) and inflation (Kruskal Wallis, $X^2 = 288.7$, $p < 0.001$) significantly differed between the 30 assemblages. The Jonckheere Terpstra test showed that median shell length ($z = 6.95$, $p < 0.001$) and inflation ($z = 13.02$, $p < 0.001$) increased with stratigraphic height in the section. Overall the body fossils (i.e. with shell) were on average 3 mm shorter, 1 mm narrower and 3 mm less inflated compared with the internal moulds (Mann-Whitney U-test, $p < 0.005$): therefore the broad stratigraphic trend of increasing size through time, is slightly underestimated (Figs 3-4). The morphometric indices revealed differences in the degree of *D. ovum* shell flexure (SDI1, Kruskal-Wallis test, $X^2 = 44.12$, $p = 0.027$) and elongation of the posterior end (SDI3, Kruskal Wallis test, $X^2 = 75.29$, $p < 0.001$) between assemblages. *D. ovum* shell posterior-anterior asymmetry (SDI2, Kruskal-Wallis Test, $X^2 = 36.13$, $p > 0.05$) did not differ between stratigraphic levels (Fig. 4).

The morphometric data were subdivided into two groups based on TOC content ($< 2\%$ or $> 2\%$ wt.) and the median shell height, length, elongation and flexure were lower when TOC was $> 2\%$ (Table 1). Thus, when TOC was high *D. ovum* shells were smaller and had greater posterior elongation and flexure.

Multiple regression showed that under conditions of low ($< 2\%$) sedimentary TOC mean shell length and width were positively correlated with TOC (Table 2). Higher TOC corresponded to larger shells presumably indicating a link with their food supply (organic matter). For maximum shell length the strongest predictor variable

was TOC/TS a proxy for palaeoredox (Table 2) with high TOC/TS indicating greater oxygenation, corresponded to larger shells. Of the geochemical proxies only TOC and TOC/TS (Pearson's correlation $r = 0.724$, $p = 0.004$, $n=30$) were correlated with each (at $p>0.01$), but this may be due to their common derivation. However, model statistics did not indicate any multicollinearity in the regressions (Table 2). All but one stepwise multiple regression showed a significant influence of TOC (Table 2) and excluded TOC/TS. It seems therefore that primary productivity had a greater effect on shell size, and any direct effects of palaeoredox were not established.

When TOC exceeded 2% multiple regression with bivalve size (mean shell length, width or maximum length) was not significant ($p<0.05$) suggesting that either: bivalve size was only related to TOC when organic matter supply was low, and thus food supply was limited, or that conditions were more reducing when TOC was $>2\%$ and this confounded the influence of food supply on bivalve growth. *D. ovum* did not occur in facies with less than $\sim 1\%$ TOC (Fig. 4). There was no correlation between bivalve density and size that might indicate intraspecific competition for resources restricted growth.

D. ovum shell length was strongly positively correlated with shell height (reduced major axis regression on log-transformed data, $R^2 = 0.48$, $t = 27.89$, $p<0.001$; $a = 1.18$) and weakly correlated with shell inflation ($R^2 = 0.18$, $t = 11.670$, $p<0.001$, $a = 0.43$) (Supplementary Information Fig. S2). The relationship between shell height and inflation was significant but very weak ($R^2 = 0.03$, $t = 4.08$, $p<0.001$, $a = 2.28$). The relative rates of growth between age-dependent morphometric variables such as these can indicate whether proportionate or disproportionate (allometric) growth occurs between the different morphometrics. The allometric

exponent (equivalent to the slope of the regression line when data are log-transformed) of the relationship between *D. ovum* shell height and shell length was >1 meaning that in *D. ovum* allometry between shell height and length was positive. Thus, *D. ovum* growth was disproportionate: with height increasing faster than length.

Shell growth patterns were examined for a small number of well-preserved body fossils to achieve an overview of *D. ovum* growth. In many cases external growth bands were prominent and numerous (e.g. Fig. 2C–E), and the most distinct (as indicated by their thickness, topography, texture and colour) were interpreted to be annuli. This interpretation of annuli is supported by the growth patterns for the *D. ovum* specimens (Fig. 5B) that fit the von Bertalanffy growth model ($R^2 > 0.99$, $p < 0.05$). Shells were aged between 7 and 9 years, and population growth rates (ω) ranged from 3.75 to 6.80.

3.3 Population structure

The length frequency distributions (LFDs) from each of the 30 assemblages showed that the *D. ovum* population dynamics varied through time (Fig. 3A). One third of the shell pavements had unimodal size distributions (the majority having a mode ≥ 16 mm), and the remainder were multimodal indicating that at most levels more than one size cohort was present. Fifteen LFDs were negatively skewed, five were approximately normal and ten were positively skewed (Fig. 3A). Both the shell length range and the number of modes increased throughout the species stratigraphic range: with most LFDs being positively skewed below 44 m (mean skew -0.06) and normal or negatively skewed above 44 m (mean skew 0.15). The LFDs of the bivalve species that dominated the seafloor at the onset (*tenuicostatum*

Subzone), during (*exaratum* Subzone) and after the Toarcian OAE (*falciferum* Subzone) are very different from those for *D. ovum* (Fig. 3B).

There were no shells in length classes <8 mm in any *D. ovum* assemblage (Fig. 3A), and there was no taphonomic evidence (e.g. sedimentary features indicating currents or shell fragments) for size selective removal of these smaller shells. However, differences in the preservation of body fossils throughout the section (Table S1) suggest some diagenetic dissolution may have occurred.

3.4 Benthic community change

In the Cleveland Basin benthic communities of the upper *falciferum* and lower *commune* subzones (between 26 m and 35 m) were dominated by the bivalve *M. substriata* with occasional occurrences of *P. dubius*, *B. buchi*, the brachiopod *L. longovicensis* and the gastropod *Ptychomphalus expansus* (Fig. 4; Little 1995, 1996). TOC content was initially high and decreased to ~ 2% TOC between 38.01 m and 41.71 m; (Fig. 4), and *D. ovum* appeared at ~38.60 m (Fig. 4). Throughout its sampled stratigraphic range *D. ovum* abundance varied 10 fold, reaching a maximum at ~41.0 m, followed by a general decline through time (Fig. 4). The abundance of the other bivalve species *B. buchi*, *M. substriata* and *G. donaciformis* (Fig. 4) increased above 44 m but these taxa were less abundant than *D. ovum* that dominated throughout the main Alum Shale.

Mean TOC decreased from 2.16% to 1.94% above 41.71 m (Fig. 4), and pyritised trace fossils appeared at 42 m, their first occurrence since before the OAE. The highest *D. ovum* abundances did not correspond with high trace fossil abundances (Fig. 4). Above 47–48 m trace fossil abundance markedly increased although remained variable.

4. Discussion

The present study explored changes within the early successional benthic communities present ~900 kyr after the end of the Toarcian OAE (based on the timescale of Kemp et al. 2011), as geochemically defined (Pearce et al. 2008), in the Cleveland Basin, Yorkshire, UK. At this time the Earth was recovering from a global warming event that was comparable with the changes predicted under the highest IPCC $p\text{CO}_2$ emissions scenario that predicts a 7.5°C atmospheric temperature rise by 2100 (IPCC, 2103). The Cleveland Basin benthos remained species poor for >900 kyr after the OAE (Caswell and Frid 2017), and the recovering seafloor communities of the *bifrons* Zone consisted predominantly of near-monospecific occurrences of the bivalve *D. ovum*. Other bivalve species were occasionally abundant. Together with the geochemical proxy data (Pearce et al. 2008; Raiswell et al. 1983) this suggests that conditions remained deoxygenated at times. Thibault et al. (2018) concluded that at least the lower half of the *commune* Subzone was dysoxic. In the upper *commune* Subzone (~42 m) macroinfauna reappeared, as shown by the presence of trace fossils. The improving sedimentary conditions coincided with a shift from near-monospecific communities of *D. ovum* to a more diverse assemblage (Fig. 4; Danise et al. 2013; Little 1996) with a greater range of life and feeding habits (Caswell and Frid 2017).

Nuculanid Jurassic deposit feeders such as *Dacryomya* and *Nuculana* spp. were geographically widely distributed during the Pliensbachian and Toarcian Stages. Both taxa predominantly occurred in mudstones and marlstones (Supporting Information Table S2), indicating a preference for organic-rich substrates. These occurrences suggest that *Dacryomya* was tolerant of low oxygen conditions (Marinov et al. 2006) similar to *Nuculana* species today (Holmes et al. 2002). *Dacryomya* spp.

Seem to have been 'enrichment opportunists' meaning that they were the initial colonizers in organic rich formerly anoxic areas (and so differ somewhat from general opportunists; Pearson and Rosenberg 1978). The occurrences of the first infaunal taxon, *D. ovum*, after the OAE are important because burrowing animals would have mixed and reoxygenated the sediments increasing the habitat available to less tolerant taxa. Thus, the establishment of burrowers, such as *D. ovum*, would have facilitated the recovery of the Toarcian benthos.

Very few broken or disarticulated shells occurred in the shell pavements suggesting generally low energy conditions and minimal post-mortem disturbance. The *D. ovum* pavements are therefore autochthonous or parautochthonous. Watson (1982) suggested that, in the upper *commune* Subzone, *D. ovum* infilled with mud matrix and oriented orthogonal to the bedding were better preserved. The data from this study supports this suggestion: above 47 m shell compaction decreased, and a higher proportion were preserved as internal moulds. This variable preservation of the aragonite shells could be due to variations in the vertical position of the redox boundary: when the boundary was at the surface the material below was less likely to dissolve because it was below the taphonomically active zone (Cherns et al. 2008; Wright et al. 2003). The lack of body fossils, and the predominance of internal moulds, above 47 m could therefore indicate changes in the vertical position of the redox boundary in the *fibulatum* Subzone. Further high resolution geochemical proxy data are needed to confirm these changes.

4.1 Palaeoecology

During deoxygenation extant burrowing animals migrate towards the sediment surface to facilitate access to oxygen, and when low oxygen conditions persist they leave their burrows entirely and live on the surface until conditions

improve (e.g. Baden et al. 1990; Long et al. 2014; Norrko and Bonsdorff 1996; Rosenberg and Loo 1988). As conditions deteriorate further they extend their appendages or entire body up into the water column to access the oxygenated water (Nilsson and Rosenberg 1994; Reidel et al. 2014; Rosenberg et al. 1991). For instance, many bivalve species have been observed to extend their siphons up into the water column during deoxygenation (Rosenberg and Loo 1988; Taylor and Egglestone 2000, Seitz et al. 2003; Tallqvist 2001). We hypothesise that *D. ovum* also behaved in this way during deoxygenation.

The morphology of *D. ovum* suggests that the usual life position would have been at shallow sediment depths with the long-axis oriented approximately vertically and the rostrate posterior and siphons projected towards the sediment surface (Stanley 1970; Stanley 1981). Observations of the brachiopod *Discinisca infraoolitica* preferentially attached to the posterior end of *D. ovum* in the upper *commune* Subzone (Watson 1982) support such a living habit. The suspension feeding epibionts all had their anterior, feeding, end oriented towards the posterior of *D. ovum* where they would have benefitted from the inhalent and exhalent currents (Watson 1982), thus the posterior ends *D. ovum* would have been habitually emerged above the sediment surface during life. *D. ovum* shells were often oriented concordant to the bedding (i. e. not in life position) and, because there was minimal evidence for post-mortem disturbance, these occurrences suggest that *D. ovum* may have adopted an epifaunal life habit at times (i.e. during bottom water anoxia).

The present study showed that, although some aspects of *D. ovum* shell shape were similar between assemblages, there were variations in the extent of posterior-anterior asymmetry and elongation of the posterior end of the shell. Such

shape changes would have been advantageous for reaching oxygenated parts of the water column during deoxygenation. For instance, in present-day hypoxic sediments *M. balthica* shells have more elongated posterior ends an adaptation that facilitates siphon extension into oxygenated water (Sokolowski et al. 2008). The posterior elongation of *D. ovum* in Yorkshire might also have been an adaptation to deoxygenation (Fig. 2B–H).

4.2 Shell size and growth

The *D. ovum* shells from the Cleveland Basin were up to six times larger than Sinemurian *Dacryomya heberti* and 3–4 times larger than Pliensbachian and Oxfordian *Dacryomya* spp. (Delvene 2000; Hodges 2000; Table 3). The mean length of *D. ovum* varied by up to 8 mm throughout its stratigraphic range in Yorkshire, although this is probably an underestimate of up to 3 mm due to the lack of a shell for most specimens (the internal moulds) in the *fibulatum* Subzone (Fig. 4). The variations in *D. ovum* size, and thus growth, could be due to density dependent factors (Olafsson 1986), changes in food supply (Beukema and Cadée 1991; Carmichael et al. 2004; Kirby and Miller 2005; Schöne et al. 2005; Thompson and Nichols 1988), temperature, salinity (e.g., Ambrose Jr. et al. 2006; Johnson 1999; Schöne et al. 2005) or deoxygenation (Long et al. 2014). *D. ovum* body size was correlated with TOC when TOC was <2%, and conditions were presumably more oxygenated, which is supported by a higher abundance of trace fossils (Fig. 4). The absence of statistical relationships between shell size and shell density, proxies for surface seawater temperature ($\delta^{18}\text{O}_{\text{bel}}$) and independent proxies for palaeoredox ([Mo], [U], Th/U, U/Th, DOP) suggest a link with organic matter and so food supply. Surface deposit feeders such as *Dacryomya* could have directly fed on labile surface organic matter or the sedimentary microbes that process it (Lopez and Levinton 1987; Levinton and Bianchi 1981). They are unlikely to have efficiently consumed the

legacy organic matter that accumulates at depth within the sediments (Levinton and Kelaher 2003; Mayer et al. 1997). So like the suspension feeding opportunists during the OAE (Caswell and Coe 2013) the *Dacryomya* may also be responding to variations in fluxes of organic matter from primary production in the photic zone.

The main influences on the TOC content of sedimentary rocks are primary production and organic matter preservation (Arthur and Sageman 1994), and the latter is primarily controlled by sedimentation rate not bottom water oxygen levels (Betts and Holland 1991). The lack of a timescale for the *bifrons* zone in Yorkshire means the influence of variations in sedimentation rate on TOC cannot be excluded, but cyclostratigraphic data from the *falciferum* and *tenuicostatum* zones suggest that sedimentation rates did not vary much (Kemp et al. 2011). The range of TOC concentrations recorded in the *bifrons* Zone are similar to the lower end of the sedimentary TOC ranges found in comparable present-day deoxygenated areas (e.g. 1.5–6.5% TOC in continental margin sediments, and 3–15% TOC in anoxic silled basin sediments; Demaison and Moore 1980; Levin and Gage 1998). Similar to *Dacryomya*, present-day seafloor communities show relationships between macrofaunal body-size and TOC: under intermediate levels of deoxygenation, taxa that are tolerant of deoxygenation show increased body size due to organic enrichment (e. g., Borja et al. 2000; Caswell and Frid 2018; Fuksi et al. 2018; Weston 1990). For instance, changes in the size of the bivalve *Corbula gibba* in deoxygenated and oxygenated areas of the Adriatic Sea over the last c. 10 ka were due to changes in TOC content (Fuksi et al. 2018) that are of a similar magnitude to those found in the present-study.

During the OAE the body size of the dominant species, *P. dubius*, in

Yorkshire decreased by up to 50%, and these changes were also linked with primary productivity (Caswell and Coe 2013). In the French and Spanish early Toarcian sections 11 bivalve species that occur in abundance after the OAE (*commune* and *fibulatum* zones) had maximum body sizes 26–82% smaller than their other Jurassic occurrences (Fürsich et al. 2001). These small sizes were interpreted to reflect stunted growth due to an inadequate food supply (Fürsich et al. 2001). Overall, it seems that considerable changes in body size occurred both during and for some time after the Toarcian OAE in the Cleveland Basin, Yorkshire, and in the mid to lower shelf environments in Spain and France, respectively and that these changes were predominantly driven by changes in primary productivity and thus food supply. On the margins of the Panthalassa Ocean, at sections exposed in Alberta, Canada, both bivalves and brachiopods exhibited body-size reductions during the OAE and remained small in the aftermath (during the *planulata* Zone which is equivalent to the *bifrons* zone)(Martindale and Aberhan 2017).

Major changes in the phytoplankton assemblage composition and microfossil body-size during and immediately after the Toarcian OAE (*falciferum* Zone; Clemence et al. 2015; Martindale and Aberhan 2017; Mattioli et al. 2008; Palliani et al. 2002; Vania et al. 2017) support the suggestion that at times food limitation restricted bivalve body-size. Collapses in primary productivity have occurred during other mass extinctions including the Late Devonian (Girard and Renaud 1996), Permian–Triassic (Twitchett 2006), Triassic/Jurassic boundary (Ward et al. 2004) and Cretaceous/Tertiary boundary (Smith and Jeffery 1998). Notable body-size decreases followed three of these events and conform to what is known as the ‘Lilliput effect’ (Urbanek 1993).

4.3 Population dynamics

In low energy environments such as those of the *bifrons* Zone, where taphonomic processes are reduced, the LFDs of brachiopod death assemblages have been shown to have high fidelity with the life assemblages (Tomasovych 2004), and so the skew and modality of the LFDs can be used to reliably infer population structure. The length frequency distributions (LFDs) of *D. ovum* were mostly indicative of mature populations with multiple size cohorts (Fig. 3B), and through time as the environmental conditions improved they became more skewed towards the larger size classes. Changes in the mean and maximum shell length also reflect this shift. However, the absence of *D. ovum* shells <8 mm across all assemblages, and the lack of any signs of physical disturbance, could suggest post mortem dissolution of the smallest shells (Dodd and Stanton Jr. 1990). However, Tomasovych (2004) showed that even when shell dissolution occurs it is incomplete and significant numbers of juvenile shells often remain. The complete absence of juveniles *D. ovum* therefore suggests it had low recruitment and/or juvenile mortality.

The LFDs of the dominant bivalves during the OAE in Yorkshire (Fig. 3B), France and Germany although different from the LFDs for *D. ovum* all showed a similar trend to that observed in this study. In Yorkshire *B. radiata* and *P. dubius* LFDs were strongly positively skewed during the OAE and the strength of the skew weakened as conditions improved (Caswell and Coe 2013). In SW Germany *B. buchi*, *P. dubius* and *M. substriata* (Röhl 1998; Röhl et al. 2001) and in southern France *Dacryomya lacrymya* (Fürsich et al. 2001) LFDs also shifted from positively skewed unimodal through to normal and/or negatively skewed multimodal LFDs after the OAE. In Alberta although this general pattern was followed there were distinct differences between taxa. *Meleagrinella* and *Bositra* exhibited strongly positively skewed LFDs *Pseudomytiloides* did not, and in strata coeval with the *bifrons* Zone in

NW Europe recovery is not apparent for *Meleagrinella* (Martindale and Aberhan 2017).

In present-day deoxygenated areas populations of tolerant bivalves have life assemblages dominated by juveniles, with LFDs that are positively skewed reflecting strong recruitment but low survival into adulthood (Long et al. 2014; Powers et al. 2005). Death assemblages from present-day deoxygenated areas may also produce strongly positively skewed LFDs reflecting high juvenile mortality (Fig. 2B). Opportunist taxa with very high fecundity, fast growth and generation times may take advantage of the brief periods of oxygenation and establish large populations very rapidly (Caswell and Coe 2013). Other tolerant bivalves for example *M. balthica* may be able to continue to reproduce during low oxygen conditions, e.g. at $<2 \text{ mg l}^{-1}$ dissolved oxygen *M. balthica* continues to reproduce although fecundity decreases by ~75%; and, at $<1.5 \text{ mg l}^{-1}$ *M. balthica* recruit but do not attain reproductive age (Long et al. 2014). Long et al. (2014) showed that present-day populations of *M. balthica* may be supported by recruitment from nearby oxygenated areas, up to some threshold beyond which the increases in the extent and duration of hypoxia results in local extinction.

The number of growth lines on *D. ovum* shells of 20 mm shell height ranged between seven and nine (Fig. 5) suggesting that, if these were annuli, *D. ovum* lived for up to 9 years which is within the range for present-day species of this family across northern temperate latitudes (Moss et al. 2017; Nakaoka and Matsui, 1994). The population structure and growth curves (Fig. 5) together suggest that *D. ovum* had the attributes of a K-strategist (i.e. one with a relatively long lifespan and low reproductive output; MacArthur 1960). Similarly, older *Dacryomya* spp. from the Sinemurian and Pliensbachian of the southwest UK have LFDs that are indicative of populations with more mature individuals (Hodges 2000). Contrastingly, *P. dubius*,

which dominated during the OAE, seems to have had an opportunistic life history and may have reproduced after just a few months (Caswell and Coe 2013).

4.4 Changes in seafloor communities

The Toarcian OAE was associated with a mass extinction of benthic and pelagic marine invertebrates across the Boreal and Tethyan realms (Aberhan 2002; Caswell et al. 2009; Cecca and Macchioni 2004; Little and Benton 1995; Ruban 2004; Voros 2002; Zakharov 2006). Across NW Europe the seafloor macrofaunal palaeocommunities were of very similar composition during the OAE being dominated by 2–3 bivalve species only throughout the *falciferum* Zone in the Cleveland Basin, UK, Paris Basin and SW German basins (Caswell et al. 2009; Fürsich et al. 2001; Riegraf 1982; Röhl 1998; Röhl et al. 2001). Furthermore, the benthic assemblages on the margins of the Panthalassa Ocean were also remarkably similar to NW Europe (Martindale and Aberhan 2017). Taxa at higher trophic levels were also affected e.g. marine reptiles and cephalopods in NW Europe (Caswell and Coe 2014; Maxwell and Vincent 2016). Subsequently, an impoverished benthos persisted across NW Europe, and as conditions improved (*commune* and *fibulatum* subzones; Fig. 4), benthic communities became dominated by species, with affinities for organic rich substrates, and a greater diversity of life and feeding habits (e.g., Caswell and Frid 2017; Danise et al. 2013; Fürsich et al. 2001; Röhl 1998). In Yorkshire the trace fossils were predominantly those of shallow burrowers with morphologies of grazers or deposit feeders (Martin 2004, Sellwood 1972).

Three ecologically significant changes are apparent, from both the body and trace fossil data from the Alum Shale of the Cleveland Basin (Fig. 4). **(1)** In the mid *commune* Subzone *D. ovum* abundance increased sharply and these populations became established. **(2)** In the upper *commune* Subzone, at 42 m, trace fossils re-

appeared, having been absent since before the start of the OAE, and body fossils of the deep burrower *Gresslya donaciformis* occurred (Fig. 4). **(3)** The degree of bioturbation markedly increased at the base of the *fibulatum* Subzone and, although variable, increased throughout the subzone. These changes show stepped improvements in conditions on the seafloor that indicate increasing oxygenation. This interpretation is consistent with the stepped decreases in TOC and a suite of other geochemical proxies that show that although conditions were generally deoxygenated in the *bifrons* Zone, oxygenation was increasing (including TS/TOC, Degree of Pyritisation of Fe, [Mo], Re/Mo and $\delta^{98/95}\text{Mo}$; Pearce et al. 2008; Raiswell et al. 1993; Thibault et al. 2018).

The temporal variations in trace fossil abundance, *D. ovum* abundance and preservation likely reflect fluctuations in the degree of oxygenation and vertical position of the redox boundary throughout much of the *commune* Subzone. Deoxygenation probably varied seasonally or episodically throughout the OAE with reoxygenation becoming more prolonged throughout the *bifrons* Zone leading to higher benthic diversity (Caswell and Frid 2017, Levin and Gage 1998). A present-day study of bioturbation along an oxygenation gradient in the Oman Margin Oxygen Minimum Zone showed that below 0.13–0.27 ml l⁻¹ dissolved oxygen burrowing was substantially reduced (Demaision and Moore 1980; Smith et al. 2000). Furthermore, benthic scavengers were absent below 0.3–0.5 ml l⁻¹ dissolved oxygen (Demaision and Moore 1980). The apparent absence, or low abundance of, both scavengers and bioturbators in the Cleveland Basin suggests that at times dissolved oxygen levels were below 0.5 ml l⁻¹.

The lack of correspondence between high *D. ovum* abundance and increased bioturbation suggests that even though *D. ovum* had an infaunal life habit it was not living infaunally below 42 m stratigraphic height (Fig. 4). The appearance of trace fossils and the increased abundance of other taxa only after *D. ovum* became established suggests it may have performed an ecosystem engineering role enabling other taxa to become resident. Further investigation of the associations between body and trace fossils could help to better understand the benthic successional changes during recovery from the OAE.

5. Conclusions

Dacyomya ovum like other members of the genus had a preference for organic rich substrates, and after the Toarcian OAE it was the first infaunal taxon to occur in abundance and so was an important pioneer species. The population structure, size and growth data suggest *D. ovum* was a K-strategist, and at intermediate levels of deoxygenation for *Dacyomya*, like tolerant taxa today, body size was linked with organic enrichment. Variations in the body size and population structure of bivalves were evident both during and after the early Toarcian event from contemporaneous sections in the UK, France, Spain, Germany and Canada; and, are similar to those observed for present-day bivalves exposed to deoxygenation. In NW Europe the body size changes were attributable to changes in the food supply of the dominant benthic taxa, and show that changes in primary productivity had a major influence on benthic ecosystems both during and after the OAE.

After the Toarcian OAE an impoverished benthos persisted across NW Europe, and as conditions slowly improved in the *commune* and *fibulatum* subzones diversity increased and benthic communities became dominated by species, with affinities for organic rich substrates, and infauna became re-established. The absence, or low abundance of, trace fossils in the lower *bifrons* Zone in Yorkshire suggest that dissolved oxygen was below 0.5 ml l⁻¹ at times. Infauna can perform

important ecosystem engineering roles and make substantial contributions to benthic ecosystem functioning. Improved understanding of the successional changes within the infaunal communities after the OAE are important for understanding the consequences of deoxygenation and the recovery processes in present-day marine ecosystems threatened by anthropogenic climate change.

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Figure captions

Fig. 1. Field study area. A. Map of the UK. Grey inset boxes show sites of *M. balthica* (northwest UK) and *D. ovum* collection (northeast UK; detail covered by B). B. Map of the Cleveland Basin showing the Lower Jurassic outcrops, showing Peak Fault (N-S oriented) to the east, and the Vale of Pickering and the Howardian – Flamborough Fault Belt (E-W oriented) to the south (modified from Rawson and Wright, 1995). Locations of the exposure from which the samples were collected between Whitby and Saltwick Bay, NE Yorkshire, UK are shown together with four other key localities with extensive early Toarcian exposure.

Fig. 2. Specimens of *Dacryomya ovum* from Saltwick Bay, N Yorkshire, UK showing A. Measurement of shell length (S-L where S is the posterior and L is the anterior end of the shell), shell height (U-V where U is umbo and V the ventral side of the shell). Additional measurements used to calculate the three deformation indices include: UA, UB, UC, UD, UE, UF, UG, UH, UI and US are the distances, at the posterior end, from the umbo to the shell margin; each line marks one tenth of the total angle between UV and US. UJ, UK and UL are the distances, on the anterior

end, between the umbo and the shell margin with each line representing one third of the total angle between UV and UL. B. Complete uncompacted *D. ovum* viewed from the right with arrows indicating annuli. C–E Complete uncompacted *D. ovum* ($h/i = 0.07, 1.16, 1.20$) showing varying degrees of posterior elongation ($SDI3 = 1.03, 1.02, 0.97$; low values indicating greater elongation) and flexure ($SDI1 = 1.05, 1.04, 0.97$, respectively; low values indicating high flexure). F. Compacted *D. ovum* showing one valve slipped inside of the other ($h/i = 1.84$), and G. same specimen view of the left valve showing small shell fractures. H. Dorsal view of uncompacted *D. ovum* specimen shown in B. Supplementary Table S3 for raw data.

Fig. 3. Stratigraphic log of the upper Mulgrave Shale and lower Alum Shale members. Ammonite biostratigraphy, lithology, bed numbers and thicknesses are from Howarth (1962). The Alum Shale Member is unconformably overlain by middle Jurassic sandstones. Stratigraphic height (m) is above base of the *Cleviceras exaratum* subzone. A. *D. ovum* shell compaction (h/i), proportion of internal moulds, and proportion orthogonal to bedding plane in each assemblage. Skew of *D. ovum* shell length and length frequency distributions throughout the species range (this study). Shell length frequency histograms for *Dacryomya ovum* from each of the 30 stratigraphic levels. † = indicates that LFDs may underestimate shell length by a small (<3 mm) amount due to the greater proportion of internal moulds in the sample. B. Shell length frequency histograms for the dominant bivalve species present in the *bifrons*, *falciferum* and *exaratum* subzones of the Whitby Mudstone Formation, Yorkshire, UK. For comparison shell length frequency histograms for present-day bivalves K-strategist and opportunists e.g. *Mya arenaria* (pooled data from 24 samples) and *Mulinia lateralis* (time averaged death assemblage), respectively (data from Emerson et al. 1988, Levinton and Bambach 1970). From top: *Dacryomya ovum* in high TOC assemblages, low TOC assemblages and across all stratigraphic levels sampled (this study); *Psuedomytiloides dubius* from the *falciferum* (post-OAE)

and *exaratum* (during OAE) subzones, and *Bositra radiata* from the *tenuicostatum* Subzone (the onset of the OAE; Caswell and Coe 2013). Ammonite zone and subzone abbreviations: *H. falcif.* = *Harpoceras falciferum* (J. Sowerby), and *C. crass.* = *Catacoeloceras crassum* Young and Bird.

Fig. 4. Stratigraphic log of the upper Mulgrave Shale and lower Alum Shale members exposed between Whitby and Saltwick Bay. Ammonite biostratigraphy and lithology are as for Fig. 3. Total organic carbon (TOC) data are combined from Harding (2004) and McArthur et al. (2008). *Dacryomya ovum* mean shell length ($\pm$ standard error), abundance, flexure (SDI1), elongation (SDI3 $\pm$ standard error), and shell clustering (this study). * = shell length in the *fibulatum* Subzone may be underestimated by ~3 mm (due to most measurements being based on internal moulds that lack a shell). Species abundances for benthic macrofossils are from Little (1995, 1996) and Caswell et al. (2009) and include seven bivalve species (*D. ovum*, *P. dubius*, *M. substriata*, *B. buchi*, *G. donaciformis*, *O. inequivalve* and *L. hisingeri*), two brachiopods (*L. longovicensis* and *D. papyracea*), the crinoid *C. wuerttenbergicus* and the gastropod *P. expansus*.

Fig. 5. Growth curves with shell height at each growth increment for six specimens of *Dacryomya ovum* collected from four different stratigraphic heights (each line represents one individual specimen) in the Whitby Mudstone Formation, Yorkshire, UK. The population growth rate (ω) for the *D. ovum* specimens ranged from 2.84 to 6.80.

Table 1. Median *D. ovum* shell morphometrics from strata with high (>2%) and low (<2%) total organic carbon (TOC, wt. %), and statistical results for low and high TOC assemblage comparisons.

Group	Mean ($\pm$ IQR)			Median ($\pm$ IQR [†])		
	Shell length (mm)	Shell width (mm)	Shell inflation (mm)	SDI [†] 1	SDI2	SDI3
TOC $\leq$ 2%	21.90 $\pm$ 5.20	14.90 $\pm$ 3.80	8.50 $\pm$ 4.45	1.03 $\pm$ 0.08	1.02 $\pm$ 0.00	1.02 $\pm$ 0.07
TOC $\geq$ 2%	19.08 $\pm$ 3.95	14.11 $\pm$ 3.36	5.30 $\pm$ 3.25	1.01 $\pm$ 0.06	1.03 $\pm$ 0.00	0.99 $\pm$ 0.07
MW test [§]	Z = -7.63, p < 0.001*	Z = -3.63, p < 0.006*	Z = -10.42 p < 0.001*	Z = -3.52, p = 0.002*	Z = -1.07 p = 0.284	Z = -4.43, p < 0.001*

*Indicates statistical significance at p<0.05; [†]SDI = Shell Deformation Index, [†]IQR = Interquartile Range,

[§]MW = Mann-Whitney U-tests.

Table 2. Results of stepwise multiple regression with mean *D. ovum* shell length, mean shell width and maximum shell length (for which two models are presented), and five proxies for primary production (TOC), palaeotemperature ($\delta^{18}\text{O}$) and palaeoredox ([U], [Mo], TOC/TS). Only significant variables are shown.

Regression model*	R ²	B ($\pm$ SE) [†]	$\beta^{\ddagger}$	t	p [§]	Tolerance	VIF	DW
Mean shell length								
TOC	0.34	5.88 ($\pm$ 2.36)	0.58	2.50	0.028	1.00	1.00	1.57
TOC/TS			0.11	.31	p>0.05	0.48	2.10	-
[Mo]			0.26	1.1	p>0.05	0.90	1.11	-
[U]			-0.12	-0.48	p>0.05	0.97	1.04	-
$\delta^{18}\text{O}$			-0.28	-1.0	p>0.05	0.70	1.44	-
Mean shell width								
TOC	0.44	3.72 ($\pm$ 1.21)	0.66	3.07	0.010	1.00	1.00	2.23
TOC/TS			0.12	0.38	p>0.05	0.48	2.10	-
[Mo]			0.07	0.30	p>0.05	0.90	1.11	-
[U]			-0.13	-0.13	p>0.05	0.97	1.04	-
$\delta^{18}\text{O}$			0.08	0.31	p>0.05	0.70	1.44	-
Max shell length								
TOC/TS	0.37	12.00 ($\pm$ 4.52)	0.61	2.66	0.021	1.00	1.0	2.29
TOC			0.30	0.88	p>0.05	0.48	2.10	-
[Mo]			0.16	0.70	p>0.05	0.99	1.00	-
[U]			0.25	0.64	p>0.05	0.36	2.79	-
$\delta^{18}\text{O}$			-0.15	0.61	p>0.05	0.97	1.03	-

*Tolerance, VIF, and Durbin Watson statistics (>0.2, <10 and between 1.5-2.5, respectively) suggest no multi-collinearity or autocorrelation in the models. [†]B ($\pm$ standard error) model coefficient indicates contribution to the model: so a 1 unit change in the predictor variable produces a change in shell size equivalent to B; [‡] β is the standardised model coefficient. [§]p<0.05 confirms there is a significant relationship with the predictor variable;

Table 3. Comparisons of maximum shell length, height, inflation, height/length (H/L) and mean height/inflation (H/I) of different Jurassic *Dacryomya* species.

Age	Species	N*	Max. shell dimensions (mm)			Max. H/L	Mean H/I
			L	H	I		
Sinemurian [§]	<i>D. heberti</i>	48	4.9	3.5	3.6	0.71	0.97
Pliensbachia [§]	<i>D. gaveyi</i>	33	8.7	6.0	5.1	0.69	1.18
Toarcian [†]	<i>D. ovum</i>	629	19.2	15.7	11.5	0.72	2.24 [†]
Oxfordian [#]	<i>D. roederi</i>	11	7.7	4.7	-	0.61	-

*N = sample size, hyphen indicates no data were available. [†]Mean reflects a mixture of compacted and uncompacted shells; those that showed no evidence of compaction had a H/I ranging from 1.10 to 1.30.

[‡]Data from this study, [§]Hodges (2000), and [#]Delvene (2000).

Highlights

- The recovery was slow benthic diversity and infauna increased gradually
- Pioneering infauna such as *D. ovum* performed important roles in benthic succession
- D. ovum* size varied with TOC, and so food supply, when deoxygenation was moderate
- Bivalve size was linked to food supply both during and after the OAE
- Primary productivity collapse was widespread during the Toarcian OAE

Figure 1

Figure 2

Figure 4

Figure 5

Figure 6

Figure 7