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Not all aragonitic molluscs are missing: taphonomy and significance of a unique shelly lagerstätte from the Jurassic of SW Britain

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The Blue Lias Formation at Lyme Regis (Dorset, UK) includes an exceptional pavement of abundant large ammonites that accumulated during a period of profound sedimentary condensation. Ammonites were originally composed of aragonite, an unstable polymorph of calcium carbonate, and such fossils are typically prone to dissolution; the occurrence of a rich association of aragonitic shells in a condensed bed is highly unusual. Aragonite dissolution occurs when pore-water pH is reduced by the oxidization of hydrogen sulphide close to the sediment-water interface. Evidence suggests that, in this case, the oxygen concentrations in the overlying water column were low during deposition. This inhibited the oxidation of sulphides and the associated lowering of pH, allowing aragonite to survive long enough for the shell to be neomorphosed to calcite. The loss of aragonite impacts upon estimates of past biodiversity and carbonate accumulation rates. The preservational model presented here implies that diagenetic loss of aragonite will be greatest in those areas where dysoxic-anoxic sediment lies beneath an oxic waterbody but least where the sediment and overlying water are oxygen depleted. Unfortunately, this implies that preservational bias through aragonite loss will be greatest in those biotopes which are typically most diverse and least where biodiversity is lowest due to oxygen restriction. □ *Ammonite, aragonite dissolution, carbonate, dysoxia, Lias, taphonomy.*

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Calcite and aragonite are polymorphs of $CaCO_3$ and are the most common skeletal biominerals in invertebrates. Aragonite dissolves at a higher pH than calcite (pH 7.8; Tynan & Opdyke 2011)) and is less likely to be preserved in the rock record. For example it has been estimated that 50% of all carbonate sediments are geologically preserved but only 10% of aragonitic grains escape dissolution (Ku *et al.* 1999; James *et al.* 2005). This preferential dissolution has implications for our understanding of carbonate productivity and the fossil record (e.g. the missing mollusc hypothesis, (Cherns & Wright 2000)). In particular, differential preservation over time and between different settings impacts upon our understanding of palaeoecological and evolutionary dynamics.

All marine sediments contain layered bacterial reduction zones. Oxygen can only diffuse into the first centimetre of sediment from the overlying water column (Ku *et al.* 1999), and respiring bacteria quickly create anoxic conditions unless there is a continuous supply of oxygen. In a marine environment bacterial sulphate reduction occurs very close to the sediment-water interface as the bacteria utilize seawater sulphate and produce hydrogen sulphide (Ku *et al.* 1999; Sanders 2003; Wheeley *et al.* 2008) as a metabolic bi-product (Eq. 1):

$$SO_4^{-2} + 2CH_2O \rightarrow 2HCO_3^- + H_2S \qquad (1)$$

The carbonic acid from (Eq. 1) can react with calcium to form calcium carbonate, increasing alkalinity, or lower the pore-water pH if no calcium is available (Eq. 2):

$$2HCO_3^- + Ca^{2+} \rightarrow CaCO_3 + CO_2 + H_2O \qquad (2)$$

The hydrogen sulphide from (Eq. 1) can react with oxygen to form sulphuric acid (Eq. 3), substantially lowering pore-water pH:

$$H_2S + 2O_2 \rightarrow SO_4^{-2} + 2H^+ \qquad (3)$$

If no oxygen is present, the hydrogen sulphide will not become oxidized and thus will not affect the

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pore-water pH (Ku *et al.* 1999). This set of chemical reactions is here termed the Sulphide Oxidation Reaction (SOR). It results in lowered pH and hence aragonite dissolution in dysoxic sedimentary environments.

Direct preservation of aragonite is rare; aragonitic skeletons are normally replaced by other minerals. Neomorphism to calcite is particularly common and can reproduce fine detail (Maliva 1998) as can replacement by silica (Wright *et al.* 2003). However, both mechanisms require aragonite to remain stable during early diagenesis.

Buffering by sediment around the aragonitic shell can inhibit early dissolution. Studies of modern systems have shown that the addition of shell material to sediment can increase the local pore water pH and prevent dissolution (Green *et al.* 2009) of both shells and bulk carbonate sediment. Alternatively, aragonite can be removed from the taphonomically active zone (TAZ) where burrowing resupplies oxygen to the sediment and lowers the pH via SOR. Removal from the TAZ can be achieved by either hardground formation or rapid burial, e.g. by density currents (Palmer *et al.* 1988; Wheeley *et al.* 2008), both of which restrict burrowing.

Herein, the genesis of a geologically unique sedimentary pavement composed of abundant large ammonites is described. The ammonites were originally aragonitic but are now preserved as calcite in the Jurassic Blue Lias Formation exposed on the foreshore west of Lyme Regis in Dorset, UK (Fig. 1). In local nomenclature the fossils occur in Bed 29 (*sensu* (Lang 1924)) within the Sinemurian, Bucklandi Chronozone (Jurassic) (Fig. 2). The bed containing the fossils lacks evidence for rapid deposition, hard ground formation or silicification. Buffering by calcareous sediment may have occurred, but the high abundance of ammonites

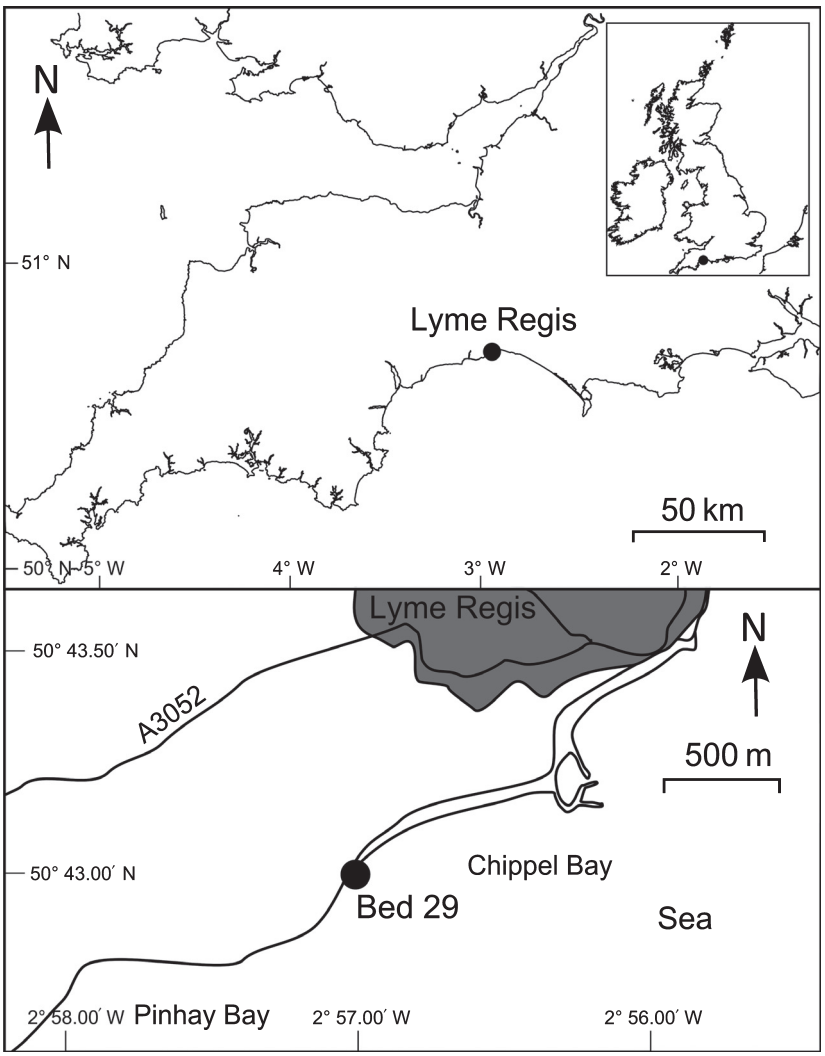

Fig. 1. Location map of the wave-washed platform of Bed 29 at Lyme Regis, Dorset, UK.

Period	Stage	Chronozone	Lithostratigraphy
Jurassic	Sinemurian	Raricostatum	Charmouth Mudstone Formation
		Oxynotum	
		Obtusum	
		Turneri	
		Semicostatum	
		Bucklandi	Blue Lias Formation
	Hettangian	Angulata	
		Liassicus	
		Planorbis	
		Tilmanni	
Triassic	Rhaetian		

Fig. 2. Lithostratigraphy and biostratigraphy of the Blue Lias Formation.

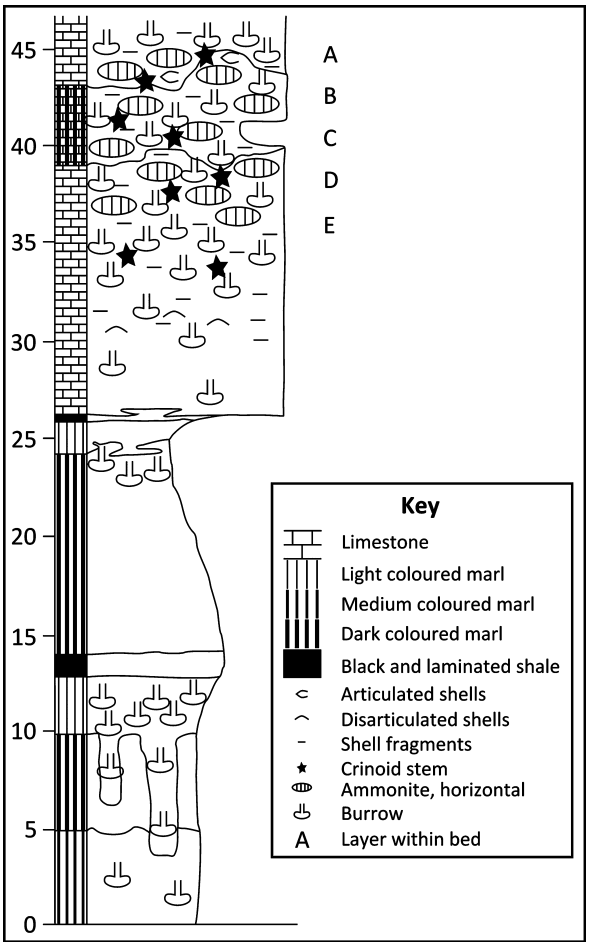

Fig. 3. Bed 29 plus beds directly below, drawn on a weathering scale. Log height in centimetres.

does not recur in other limestone beds in the sequence, which implies that other mechanisms were involved. Following a restudy of this bed, a new model has emerged for aragonite preservation in a cyclic oxic-anoxic carbonate environment which provides both an explanation for observations within this bed, and broader insights into aragonite preservation.

Geological setting

The Blue Lias Formation (Late Rhaetian–Early Sinemurian) (Fig. 2) was laid down in a shallow epicontinental sea at about 30–35° North (Ambrose 2001; Mitchell *et al.* 2010). It is approximately 26 m thick, and comprises decimetre-thick beds of black shale, marl and diagenetic limestone, each with differing levels of bioturbation and carbonate content (Lang 1924; Hallam 1960; Weedon 1985; Moghadam & Paul 2000; Arzani 2006). The limestones occur as persistent beds and impersistent concretionary horizons.

Bed 29 is a 0.18-m-thick limestone bed approximately 18 m above the base of the formation, exposed as a large wave-washed platform west of Lyme Regis (N50°42.96917 W002°57.07800 ± 5 m). It contains a 0.08 m layer (Fig. 3), characterized by large (up to 0.7 m diameter) ammonites that cover up to 40% of the wave-washed surface (Fig. 4). Other macrofauna within the bed include disarticulated crinoids, shell fragments of brachiopods and bivalves, ichthyosaur remains, echinoid spines and gastropods. Trace fossils include, in descending order of area covered, *Chondrites*, *Thalassinoides*, *Rhizocorallium, Diplocriterion* and *Rosallia*.

Methods

The wave-washed platform of Bed 29 is being eroded at a low-angle through the bed, creating a sub-planar surface exposing a cross-section through the ammonite-bearing part of the bed. This allows detailed faunal, ichnofaunal and taphonomic census data to be collected from multiple quadrats (within layers A–E, Fig. 5) across the surface.

Of the five layers sampled, E was the stratigraphically lowest, at approximately 8 cm from the base of the limestone bed; D was at approximately 10 cm; C at approximately 12 cm; B at approximately 14 cm and A at approximately 16 cm. The surface of the quadrats were wetted to enhance contrast and visibility.

Two quadrat-based studies were conducted, recording data on macrofauna and ichnofauna,

respectively. The former used 2.25 m^2 quadrats; all macrofauna present in each were recorded, together with the outer whorl diameter measurement for all whole ammonites within the quadrat, number of shell and ammonite fragments, crinoid debris and vertebrate material. For shells which overlapped the walls of the quadrat, those overlapping the north-side and west-side were included in the count, whereas those overlapping the east-side and south-side were not. The number of ammonites with any amount of spar filling was also recorded for each quadrat.

The ichnological study utilized five randomly positioned 0.01 m^2 quadrats in each layer A-E; for each ichnotaxon present, percentage cover, size, sediment fill and crosscutting relationships and burrowing interactions were recorded.

Observations

The ammonites in Bed 29 are preserved three-dimensionally and neomorphosed to calcite; the septa are generally still in place. Most are preserved horizontally, and, like all fossils in Bed 29, show no preferred orientation. Ammonites are mainly sediment-filled, with sporadic spar-filling restricted to layers B and C (Fig. 6), where it occurs in 37–45% of individuals. Size distribution for the whole bed follows a biologically typical population distribution (Fig. 7) with a greater number of smaller individuals.

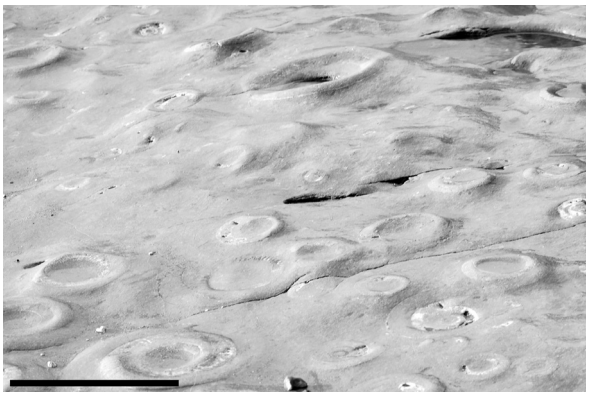

Fig. 4. Wave-washed ammonite pavement within Bed 29, west of Lyme Regis. Scale bar approx. 20 cm.

All quantitative data from layers A–E correlate strongly with position within the bed, specifically with 'centrality', i.e. the distance from the top or bottom of the bed (r-values given herein for correlation are Pearson's product-moment coefficients). Ammonite size, for instance correlates inversely with centrality ($r = -0.81$), while ammonite specimen density correlates positively ($r = 0.92$) (Fig. 6). Many ammonites, including spar-filled individuals, are 'unroofed' (Fig. 8A), i.e. missing the upward-facing side of their shell.

The colour and bioclast content of the sediment infill of some ammonites differs between chambers, and frequently from the surrounding sediment (Fig. 8B, C). Large bioclasts, including articulated crinoid-stem sections, are present within inner whorls, even where septa are still in place (Fig. 8D). The distributions of shell fragments, ammonite fragments and calcitic spar-filled ammonites all correlate positively with centrality ($r = 0.80$, 0.78, 0.78, respectively). Epibionts are absent although scattered crinoid debris occurs around some ammonites.

Thin sections through an unroofed ammonite show the removal of the upper part of the shell was by dissolution not abrasion: the break in the shell is not sharp, and occurred before neomorphism to calcite (calcite crystals are undamaged, Fig. 8E). The bioclast size and content within the ammonite

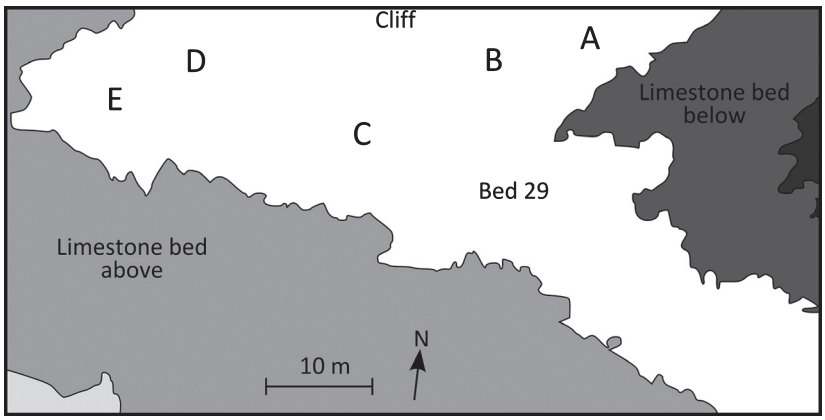

Fig. 5. Map of the layer outcrop in relation to the wave-washed platform of Bed 29 (mapped June 2012). Map centred around N50°42.96917 W002°57.07800 ± 5 m. Due to the angle of erosion of the wave-washed platform, the surface of the platform cuts through Bed 29 at a shallow angle with layer E lowest in the Bed and layer A the highest.

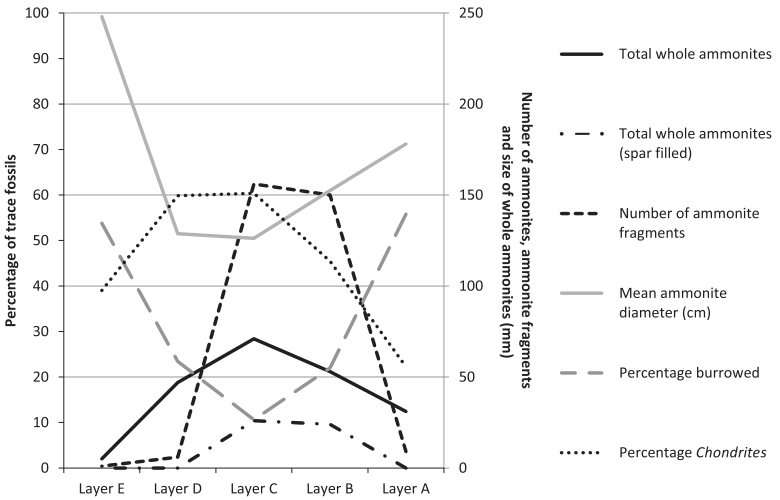

Fig. 6. Summary graph of the bioclast and trace fossil variation through Bed 29. Layer E is lowest in the Bed, layer A is highest.

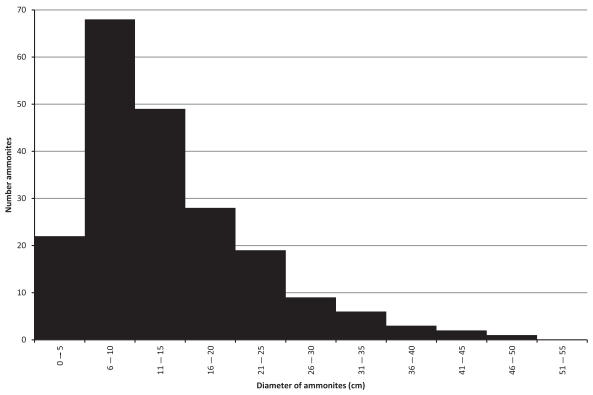

Fig. 7. Histogram showing ammonite diameter size distribution observed within Quadrats A–E.

differs from that without. All other aragonitic fossils in thin section are also preserved as calcite.

Within the bed, trace fossils are sharply defined but unwalled, and are filled with differing coloured sediments which, coupled with cross cutting relationships, suggests at least four phases of burrowing. Burrowing intensity correlates inversely with centrality ($r = -0.96$), whereas *Chondrites* becomes more dominant (measured as a proportion of all ichnofossils) in the centre of the bed ($r = 0.84$, Fig. 6). *Chondrites* is occasionally found within ammonites, generally in the body chamber, although it also occurs restricted to individual chambers in the inner whorls.

Sedimentary environment

During deposition sediment was firm, allowing creation of sharp, unwalled burrows. The carbonate mud lithified early, preventing compaction and preserving three-dimensional shells and burrows. Unroofing of ammonites must have occurred after settling (the breach is always on the uppermost side), and, where spar-filled, these specimens imply multiple phases of erosion and deposition: for spar to grow, they must have been buried whole before being uncovered and unroofed. A long time period allowing for erosion and deposition is also supported by the many different sediment types, differing in composition and bioclast content, which are recorded within the bed.

Different sediment fills in adjoining chambers and the restriction of *Chondrites* to individual chambers indicate that the unroofing by dissolution was an episodic process. The increased density of shell and ammonite fragments in the middle of the bed (Fig. 6) implies a decrease in sedimentation rate and an increase in winnowing during bed accumulation.

Where ammonite density is high ichnofossils, except *Chondrites,* are few (see above); this may reflect an 'armouring' effect, where numerous ammonite shells selectively inhibited larger burrows. *Chondrites* is known to be relatively tolerant of low-oxygen conditions (Bromley & Ekdale 1984), thus a second (but not mutually exclusive) interpretation is that this pattern reflects local variations in conditions in the seaway that controlled both oxygen levels and ammonite density. This is consistent with the decrease in average ammonite diameter in the middle of the bed, possibly indicating less ideal living conditions for the ammonites, such as a more restricted food source.

Ammonite accumulation

The high abundance of ammonites in Bed 29 is unusual, both within the formation and elsewhere in the

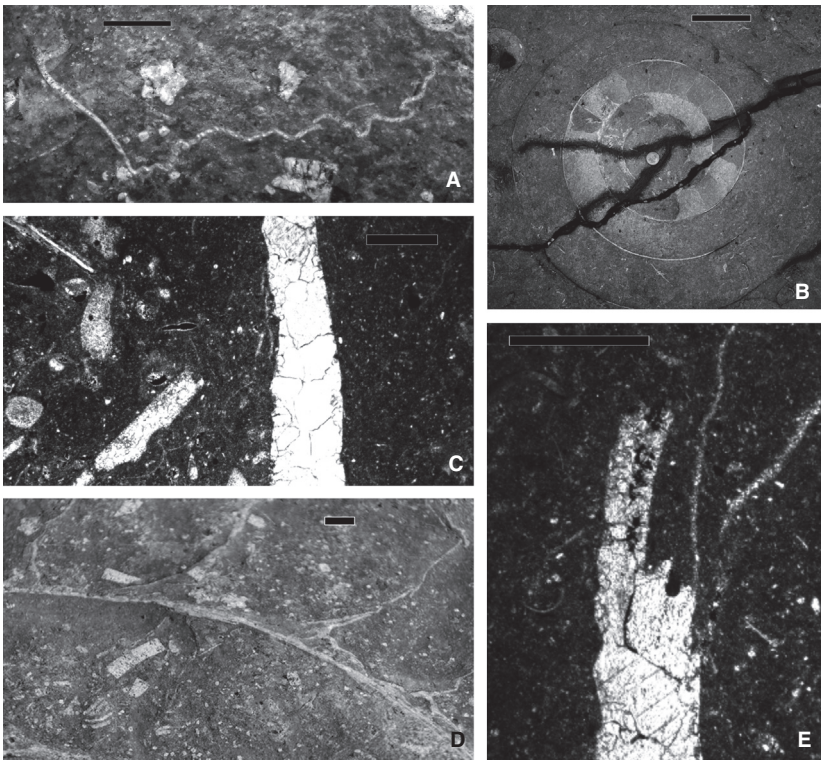

Fig. 8. A, cross-sectional view through an 'unroofed' ammonite within Bed 29, scale 10 mm. B, different bioclast content and sediment fill between conjoining chambers within a single ammonite, scale 100 mm. C, thin section showing variation in bioclast content within an unroofed ammonite (right) compared to the surrounding sediment (left), scale 0.5 mm. D, large articulated sections of crinoid stem within the inner whorls of an ammonite with the septa still intact, scale 10 mm. E, thin section showing the terminus of the shell on an unroofed ammonite, scale 0.5 mm.

geological record, making this a concentration lagerstätte. Many modern cephalopods, such as *Loligo opalescens*, congregate for breeding and die shortly thereafter (Summers 1971). However, the range of shell diameters (Fig. 7) in Bed 29 suggests that the ammonites represent a wider population sample than solely breeding adults. Additionally, *post-mortem* ammonite shells likely floated (Reyment 2008) rather than sank to the seafloor at place of death, so an accumulation of shells at a breeding site appears unlikely. Floating ammonite shells might conceivably have been rafted together by currents prior to sinking. This model would, however, predict encrustation by epibionts on both flanks (Reyment 2008); this is not observed in Bed 29, where direct evidence of encrustation is absent. Size-sorting might also be expected in a current-mediated accumulation, and is not observed. The range of ammonite shell sizes preserved may suggest a mass mortality of a whole population. However, this would require the local area to have supported an unfeasibly dense population.

By elimination, therefore, a period of stratigraphic condensation is the most plausible explanation for the high density observed within this bed, although other authors (e.g. Doyle & Macdonald (1993) and references contained within) have noted how the other mechanisms have affected other shelly accumulates. The condensation of Bed 29 is supported by multiple periods of burial and exhumation, indicated by 'unroofed' ammonites infilled with dogtooth spar, multiple phases of burrowing, and the presence of shell and ammonite fragments.

Preservation models

Preservation of aragonite at a time of sedimentary condensation is counter-intuitive because it implies increased residence time in the TAZ and more time for aragonite dissolution by SOR. Current aragonite preservation models require the aragonite to be rapidly buried to a depth where oxygen cannot be added, thus limiting SOR. The alternative mechanism presented here involves the aragonite skeleton residing on the sediment surface within an anoxic water column.

Stratification occurs where a density differential exists within a seaway; this can be caused by temperature or salinity. Where there is a large density difference over a short distance an effective barrier is formed, which oxygen cannot easily cross. Under

these conditions the lower part of the water column becomes anoxic: bacteria living below the barrier deplete oxygen by respiring, and oxygen diffusing into the surface waters cannot move past the density barrier to replenish it. Surface-water productivity is also reduced as the density barrier restricts nutrient circulation as well, so when organisms die and sink below the stratification boundary, those nutrients become unavailable to the food chain.

In a stratified ancient seaway, SOR would not have occurred as oxygen was limited, and hence aragonite would not have been dissolved. While these anoxic conditions would have excluded benthic organisms from the seafloor, nektonic ammonites could still have lived in the oxygenated upper water column, and once their shells sank below the stratified boundary they would have had a higher preservation potential. When causal factors for stratification weakened, the seaway would have returned to a mixed state, with oxygenated bottom waters. Benthic and infaunal organisms could then have colonized the seafloor, but SOR would also have resumed, creating a more corrosive environment with a lower pH.

The Blue Lias Formation reflects a cyclic oxic-anoxic environment with a low overall diversity of shelly benthos, limited but stratigraphically variable bioturbation, ichnofauna and tiering, and varying levels of organic carbon preserved in shales and marls (Hallam 1960). Bed 29 is condensed compared to other limestone units in the Blue Lias, and varying oxygen conditions are recorded within the bed itself. The conditions described above hence applied; during anoxic periods ammonite shells would have accumulated on the seafloor and become covered in carbonate sediment, allowing calcite spar to grow. When oxygenated conditions returned, burrowing and colonization by crinoids, brachiopods, gastropods and bivalves occurred, and SOR resulted in dissolution of the upper side of ammonite fossils (where exposed by current action), different sediments filled the chambers, organisms burrowed selected chambers and large bioclasts entered the inner whorls (Fig. 9). Restriction in food supply during periods of stratification may have affected ammonite growth, and could explain the average shell size decrease in the middle of the bed, which coincides with the highest density of preserved ammonites (Fig. 6). The 'centrality' variable with which much of our data correlate may hence correspond to the proportion of time for which the seaway was stratified; if so, this proportion was higher during the deposition of the centre of the bed.

While stratified conditions prevailed, ammonite shells would have accumulated within the sediment. As noted above, this may have provided an armouring effect that would have reduced the preponderance of large burrows, even after the seaway returned to a mixed state. A taphonomic feedback loop is proposed where ammonite accumulation restricted burrowing and hence reduced oxygen supply to the sediment, resulting in less aragonite dissolution through SOR and the preservation of more ammonites. A further feedback loop may have resulted from carbonate buffering: as some aragonitic shells began to dissolve, the released carbonate would have raised the pH, inhibiting further dissolution.

Discussion

Seasonal stratification is very common in Recent coastal waters, controlled by temperature differences between the surface and bottom waters. It occurs in most modern carbonate shelves such as Florida Bay (Porter *et al.* 1999), Yucatan Shelf (Merino 1997) and the Great Barrier Reef (Andrews & Gentien 1982). These shelf areas are much smaller than ancient epicontinental seas which covered much of Europe and North America during the Jurassic and Cretaceous periods. Modern seas have greater connectivity to the open ocean, providing greater potential for tidal mixing which in turn reduces the extent of stratification and bottom water-water anoxia (Allison & Wells 2006). However, in larger epicontinental seas, seasonal stratification may have lasted longer and had a greater influence on the bottom water oxygenation.

Our model for Bed 29 emphasizes possible differential dissolution rates, and therefore accumulation rates, of carbonate systems in oxic as opposed to anoxic systems, and highlights the risks of using different limestone bed thicknesses to estimate primary carbonate production in an ancient seaway. Although evidence for this new model is based on observations primarily of aragonitic fossils, SOR in cyclic oxic-anoxic conditions would also affect aragonitic sediment, the dominant source of which is shelly bioclasts (Morse *et al.* 2007). However, evidence showing the effect of SOR on aragonitic sediment preservation is harder to observe due to recrystallization during neomorphism.

Within cyclic oxic-anoxic systems, nektonic aragonitic organisms also have a higher preservation potential than their benthic counterparts who can only colonize during more corrosive oxic periods. This bias would skew the ecological signal, affecting palaeodiversity estimates and possibly mask evolutionary and mass extinction patterns due to

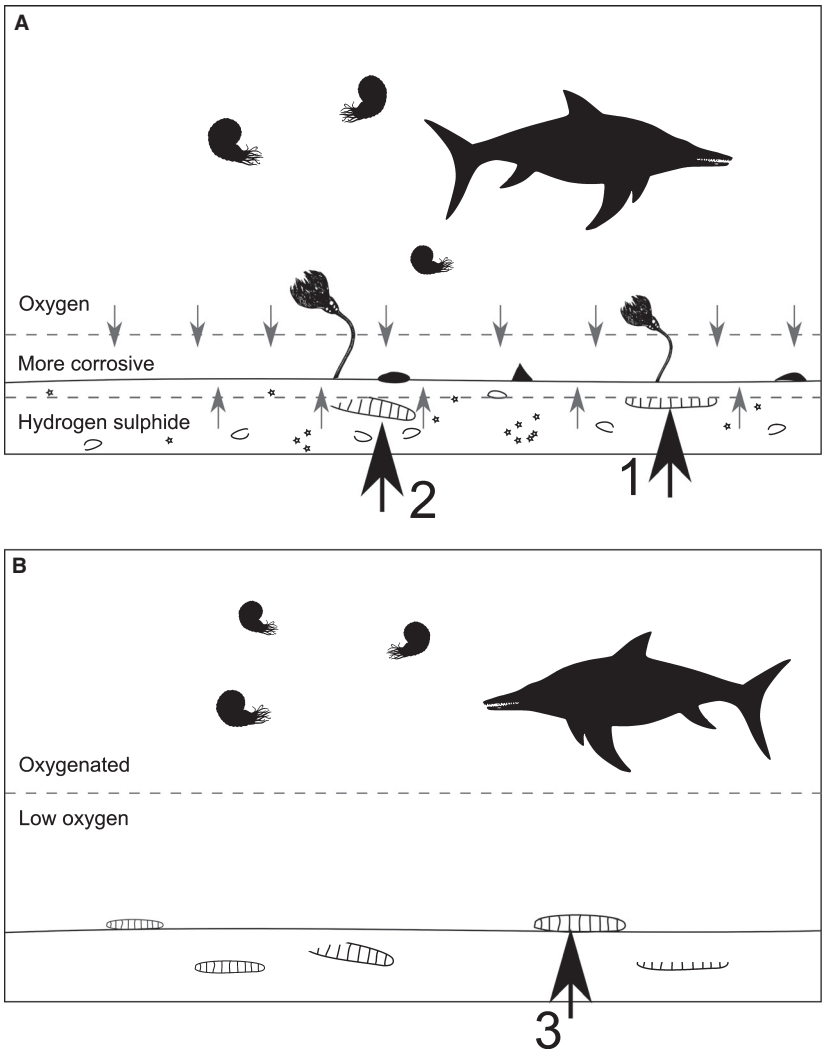

Fig. 9. Environmental reconstruction of the Sulphide Oxidation Reaction (SOR) model. A, during oxygenated conditions, benthic colonization and burrowing occurs, with nektonic creatures inhabiting the upper water column. Hydrogen sulphide from the sediment reacts with oxygen in the water column, lowering the pH at the sediment-water interface, dissolving aragonite not buffered by carbonate sediment. 1, dissolving (unroofed) ammonite. 2, angled ammonite, partially dissolving, exposing some chambers. B, during periods of stratification, the amount of oxygen in the lower water column decreases, restricting both the dissolution of aragonite and benthic colonization. 3, preserved ammonite during anoxic cycle. If covered with sediment it will be preserved whole.

preferential dissolution of aragonitic organisms in certain settings.

Conclusions

New insights into aragonite preservation in cyclic oxic-anoxic carbonate environments are presented based upon a new preservational model for a geologically unique accumulation of ammonites at Lyme Regis, Dorset. With changing oxygen conditions, the pH of the pore waters would vary, thus affecting the rate of aragonite dissolution, which in turn has lasting consequences on the geological record and implications for the fossil record (Cherns & Wright 2000), and carbonate sediment preservation (James *et al.* 2005). As cyclic oxic-anoxic environments were probably common in the epicontinental seas which have covered much of the globe throughout geological history, this new model has broad impact on our understanding of invertebrate palaeoecology and biodiversity and carbonate system dynamics.

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