

## BENTHIC ECOSYSTEM DYNAMICS FOLLOWING THE LATE TRIASSIC MASS EXTINCTION EVENT: PALAEOECOLOGY OF THE BLUE LIAS FORMATION, LYME REGIS, UK



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The Blue Lias Formation of southwest UK records the evolution of a marine, shelf ecosystem following the Late Triassic extinction event. In order to investigate responses of the local palaeocommunity to environmental changes during this critical interval in Earth history, a quantitative palaeoecological analysis of the well exposed, fossiliferous and historically important sedimentary succession between Pinhay Bay and Lyme Regis, southern England, was undertaken. Quantitative palaeoecological data were collected from 19 limestone beds of the Rhaetian-Sinemurian Blue Lias Formation. For each sampled bed, all macroinvertebrate fossil remains found within two 50 x 50 cm quadrats placed on the exposed bedding plane surface were counted and identified. Palaeoecological changes were assessed through analyses of diversity, richness, evenness, abundance and occupation of ecospace. There is a general trend from palaeocommunities with low diversity, richness, abundance and evenness around the Triassic/Jurassic boundary to those with higher diversity, richness, abundance and evenness in the late Hettangian, but there are intervals of relative stasis as well as significant shifts within biozones and even between adjacent beds. Most of the Rhaetian-Hettangian palaeocommunities are dominated by low-level, surficial, suspension feeders, but the appearance of higher- and deeper-tier organisms, and an increase in motility and feeding styles, characterise key stages of post-extinction recovery. The earliest Sinemurian assemblages show a return to low diversity, low evenness assemblages, but with high abundance. Where there is a stratigraphic overlap, the palaeoecological changes recorded in this study are comparable to those recorded from other southwest UK sites, despite differences in sampling methodology, and are mirrored by changes in the trace fossil assemblages. Local palaeocommunities were probably responding to local and global environmental and climatic changes, perhaps driven by changes in atmospheric CO<sub>2</sub> through the aftermath of the Late Triassic extinction event.

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## INTRODUCTION

The Late Triassic mass extinction is considered to be the fourth largest such event of the Phanerozoic (Hallam, 1990), and resulted in the final disappearance of taxa such as the ceratite ammonites and important bivalve and brachiopod groups, and the overall loss of 24.3% of marine families (Benton, 1995). In terms of its ecological impact, the extinction is ranked as the third most important of the Phanerozoic (Sheehan, 1996; McGhee *et al.*, 2013), and is the most significant event to have impacted post-Palaeozoic marine ecosystems. Previous hypotheses of an extraterrestrial cause (e.g. Olsen *et al.*, 1987; Ward *et al.*, 2001) have been rejected following revised dating of proposed impact craters and ejecta (Walkden *et al.*, 2002), and environmental and climatic changes resulting from massive volcanism in the Central Atlantic Magmatic Province (CAMP) are now considered the most likely causes of the extinction (Marzoli *et al.*, 1999, 2004; Wignall, 2001a; Pálffy *et al.*, 2002; Pálffy, 2003).

The timing of CAMP volcanism and the Late Triassic mass extinction are closely linked (Blackburn *et al.*, 2013), with volcanism being invoked as the cause of major changes in atmospheric conditions during the Late Triassic. The input of

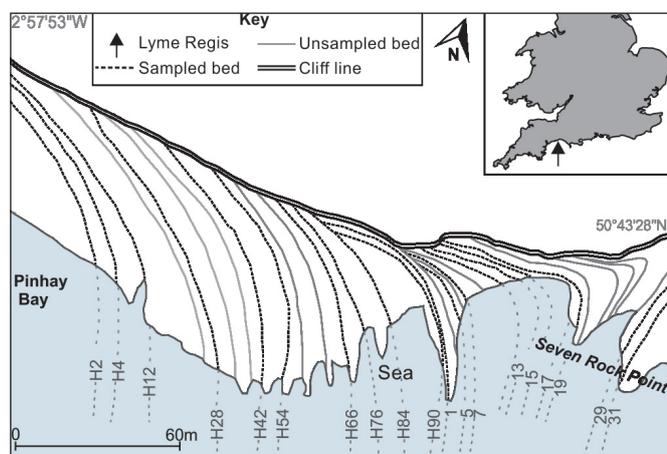
significant amounts of carbon dioxide into the atmosphere during outgassing from CAMP may explain the dramatic rise in atmospheric CO<sub>2</sub> levels inferred from palaeobotanical (McElwain *et al.*, 1999; Steinthorsdottir *et al.*, 2011) and palaeosol (Schaller *et al.*, 2011) proxies across the Triassic/Jurassic boundary. Beerling and Berner (2002) estimated that up to ~8,000-9,000 Gt of CO<sub>2</sub> and ~500 Gt of methane may have been released, which would have led to a rapid global warming. Elevated CO<sub>2</sub> and global warming would have had a number of environmental consequences for marine ecosystems, such as sea-level rise, reduced ocean circulation, expanding hypoxia, elevated weathering, runoff, nutrient influx and sedimentation rates, as recorded for other warming-related biotic crises such as the Late Permian mass extinction (Jaraula *et al.*, 2013).

Despite the importance of the Late Triassic event for the early evolution of modern-style ecosystems, relatively few studies have documented in detail the palaeoecological responses of marine ecosystems to this crisis. High resolution palaeoecological studies of the Triassic-Jurassic benthic macrofauna have previously been undertaken in southwest UK

locations such as St Audrie's Bay and Lavernock Point (Mander *et al.*, 2008). That study focused mainly on the extinction and immediate aftermath, and the analyses did not encompass the entire post-extinction recovery interval, which on trace fossil evidence extends to the late Hettangian (Twitchett and Barras, 2004). The aim of this present study is to complete a quantitative palaeoecological analysis of the benthic macrofauna of the Blue Lias Formation from the historically important and well known successions exposed between Pinhay Bay and Lyme Regis, southwest UK. Previous palaeoecological work on the Blue Lias Formation of that location comprises detailed trace fossil analyses (Moghadam and Paul, 2000; Twitchett and Barras, 2004; Barras and Twitchett, 2007) and studies of ammonites (Paul *et al.*, 2008). This study is thus the first to assess changes in the benthic macrofauna of this locality, and the first such study of the entire Hettangian post-extinction recovery interval.

## GEOLOGICAL SETTING

The study site is located about 2.5 km west of Lyme Regis, extending from the western end of Pinhay Bay eastwards around the bay to Seven Rock Point (Figure 1). Upper Triassic rocks of the Langport Member (Lilstock Formation) are exposed at the western end of the section and are conformably overlain by the Blue Lias Formation. This latter formation comprises rhythmically bedded limestones, marls and mudstones, cropping out in the cliffs and on wave cut platforms on the foreshore. Deposition took place below wave base, in an open shelf setting, as shown by the abundant and well-studied trace fossils (Moghadam and Paul, 2000; Barras and Twitchett, 2007) which can be assigned to Seilacher's (1964) Cruziana Ichnofacies.



**Figure 1.** Location of studied section from Pinhay Bay to Seven Rock Point, South-West England. Limestone beds from which data were collected are shown by dashed grey lines with accompanying bed numbers in accordance with Lang's (1924) scheme. Light grey lines represent other, unsampled, limestone beds.

The sedimentary facies of the Blue Lias Formation at this locality have been well documented (e.g. Lang, 1924; Hallam, 1964; Hesselbo *et al.*, 2004). Limestone beds may be planar, nodular, uneven, laminated or wavy, and the intervening mudstone beds may be dark, organic-rich siltstones, paper shales, or pale grey, blocky and bioturbated. These alternating carbonate- and organic-rich lithologies are representative of well oxygenated and oxygen-depleted environments, respectively (Hallam, 1964). Evidence of oxygen-restriction includes the occurrence of pyrite framboids within finely laminated shales, with the intensity of the anoxic episodes declining up-section (Wignall, 2001b). Within the limestone beds, the presence of bioturbation signifies a well oxygenated seafloor, with only a few of the lowest limestone beds in

succession lacking trace fossils (Barras and Twitchett, 2007). The oxic-anoxic alternations do not always correspond precisely to the limestone-mudstone cycles of the Blue Lias Formation, and although long debated (e.g. Hallam, 1964), it is likely that climatic and oceanographic changes driven by Milankovitch cyclicity controlled carbonate deposition and limestone formation, which was enhanced by diagenetic processes (Weedon, 1986; Moghadam and Paul, 2000). The Blue Lias Formation is biostratigraphically well constrained by a series of ammonite zones and subzones, which can be correlated globally. A ratified Global Stratotype Section and Point (GSSP) has been determined for the Triassic/Jurassic boundary and is located in the Northern Calcareous Alps, Austria (Hillebrandt *et al.*, 2013). Although the boundary-defining ammonite species is not recorded in southwest UK, the position of the Triassic/Jurassic boundary can be well constrained using palynology (Mander *et al.*, 2013), and falls within the lowest Pre-Planorbis Zone, which lacks ammonites. The remaining Hettangian succession is divided into three successive ammonite zones (the *P. planorbis*, *A. liasicus*, and *S. angulata* zones, respectively) and the youngest zone of the Blue Lias Formation sampled in this study comprises the Sinemurian *C. bucklandi* Zone.

## METHODOLOGY

A graphic log was produced by ACP and JRB, and the lithostratigraphic scheme of Lang (1924) was adopted. Lang (1924) divided the sedimentary succession into two: a lower part, with beds numbered H1-H90, spanning from the base of the Pre-Planorbis Zone to near the base of the *S. angulata* Zone, and an upper part numbered 1-51, ranging from the *S. angulata* Zone to the *C. bucklandi* Zone. Quantitative palaeoecological data were collected from nineteen of these beds by using 50 x 50 cm (i.e. 0.25 m<sup>2</sup>) quadrats. Limestone beds exposed on the foreshore were selected at random where exposure on bedding plane surfaces was good enough to allow two 0.25 m<sup>2</sup> quadrats to be placed (total sampled area per bed of 0.5 m<sup>2</sup>). For each bed, all fossil specimens found within the two quadrats were counted, measured and identified as far as possible.

Two quadrats were analysed per bed in order to sample as many of the exposed, safely accessible, limestone beds as possible through the entire succession. Although using a single quadrat per bed would have enabled sampling of more (poorly exposed) beds, this would have resulted in smaller individual sample sizes with an associated reduction in data quality. For comparative purposes, it is essential that sampling effort (i.e. the number of quadrats analysed) per bed is held constant through the studied interval. The first quadrat was placed as close to the cliff section as possible, where exposure was usually best, and the second was positioned randomly elsewhere in an attempt to reduce bias due to sample location and fossil patchiness. Throughout the lower Jurassic succession of the Dorset coast there is no evidence of large-scale geological biases associated with sedimentary rock volume, outcrops or exposures (Dunhill *et al.*, 2012), and thus the method used to control sampling effort is deemed appropriate for this small-scale field study.

Within each quadrat all taxa were identified to species level, where possible, and counted. In order for a specimen to be counted, at least 50% of the specimen had to lie within the quadrat. Any fossils that could not be identified in the field were collected, prepared in the laboratory, cleaned and identified if possible. Fossils that could not be identified to genus level were recorded as indeterminate and were included in the relative abundance, diversity and ecospace analyses as individual taxa, but were not used in the analyses of stratigraphic ranges.

The minimum number of individuals (MNI) approach was used for palaeoecological analysis, rather than relying on raw bioclast count which may overestimate the importance of

animals with multielement skeletons. Individual valves for bivalves and brachiopods were treated as representing one individual. Similarly, each ammonite specimen was counted as one individual. On the assumption that disarticulated crinoid ossicles and echinoid spines had been significantly dispersed, minimum numbers of individuals were estimated by assuming that ten individual ossicles or spines represented one living animal. Four different palaeoecological metrics were calculated, based on estimates of the minimum number of individuals present: abundance, richness, evenness and diversity. Abundance reflects the total MNI per sample, and richness is a simple count of the total number of different taxa recorded in a sample. Each taxon MNI estimates for each of the taxa present in a sample were used to calculate evenness and diversity using the statistical program PAST (Hammer *et al.*, 2001), where Simpson's diversity index was chosen as the measure of diversity. The Simpson index of diversity ranges from zero (one taxon dominates the community completely) to one (all taxa have equal abundances) and reflects the probability that two randomly selected individuals from the sample will belong to different species. The palaeoecological metrics were calculated for every sample, although it is recognised that results from samples with abundances of less than 20 MNI should be treated with caution.

Confidence intervals of 80% and 95% have been constructed for taxon ranges using the technique proposed by Marshall (2010). This approach attempts to provide an estimate of the 'true temporal range' of taxa based on known sampling, assuming factors such as constant environment, sedimentation rate and facies. Confidence intervals reflect the incompleteness of stratigraphic ranges and allow a scientific test for the predicted occurrences of taxa. Future sampling, such as increasing the number of quadrats on a sampled bed or sampling more beds, would allow for more refined models of stratigraphic range. The inclusion of published occurrences further improves the reliability of these confidence intervals.

The occupation of ecospace was assessed using the model and concepts of Bambach *et al.* (2007). The tiering level,

feeding strategy and motility of each recorded taxon was determined (Table 1) using modes of life established for the same taxa in Mander and Twitchett (2008). The data were then pooled for each ammonite zone, and relative proportions, based on the number of taxa in each zone, of the different categories of tiering, motility and feeding were then calculated, following the approach of Bush *et al.* (2007).

## RESULTS

### *Relative abundance and diversity*

The Pre-Planorbis Zone records faunal assemblages with low abundance and species richness, with no more than four species recorded in a single bed within the zone (Figure 2). The oyster *Liostrea hisingeri*, a surficial, suspension feeder, has the highest abundance and is the dominant species within most beds, resulting in an overall low evenness throughout this zone. The second most abundant species within the zone is *Modiolus minimus*, a semi-infaunal bivalve, occurring in two out of the three selected limestone beds (Figure 2).

Diversity increases within the *P. planorbis* Zone (Figure 3), to a maximum of six species recorded in a single limestone bed and remains similar throughout the *A. liasicus* Zone, with only very minor fluctuations in calculated diversity. Within the *P. planorbis* Zone, *Liostrea hisingeri* remains relatively abundant, but with a lower dominance than in the previous zone due to the appearance of *Plagiostoma gigantea*. This zone is characterised by the relatively high abundance of echinoids, the appearance of *P. gigantea*, and presence of ammonites, brachiopods (*Calcirhynchia calcaria*) and crinoids.

Notably larger fluctuations in diversity begin at the boundary between the *A. liasicus* and *S. angulata* zones. The *S. angulata* Zone records high abundances and the highest species richness, with nine species recorded in bed 7c, including the appearance of the infaunal bivalve *Pholadomya* sp. This zone also records the highest evenness (bed 1) and diversity (bed 17) recorded within this study (Figure 3). *Calcirhynchia calcaria* increases in abundance

Mode of Life			
Taxa	Tiering	Motility	Feeding
<i>Liostrea hisingeri</i>	Surficial	Non-motile, attached	Suspension
<i>Plagiostoma gigantea</i>	Surficial	Facultative, attached	Suspension
<i>Pseudolimea</i> sp.	Surficial	Facultative, attached	Suspension
<i>Calcirhynchia calcaria</i>	Surficial	Non-motile attached	Suspension
<i>Chlamys</i> sp.	Surficial	Facultative, attached	Suspension
<i>Pleuromya</i> sp.	Infaunal	Facultative, unattached	Suspension
<i>Pinna</i> sp.	Semi-infaunal	Facultative, attached	Suspension
<i>Pteromya tatei</i>	Infaunal	Facultative, unattached	Suspension
<i>Modiolus minimus</i>	Semi-infaunal	Facultative, attached	Suspension
<i>Gryphaea obliquata</i>	Surficial	Non-motile, unattached	Suspension
<i>Gryphaea arcuata</i>	Surficial	Non-motile, unattached	Suspension
<i>Gryphaea</i> sp.	Surficial	Non-motile, unattached	Suspension
<i>Pholadomya</i> sp.	Infaunal	Facultative, unattached	Suspension
Ammonite	Pelagic	Freely	Predatory
Crinoid	Erect	Non-motile, attached	Suspension
Echinoid	Surficial	Motile, unattached	Grazing

**Table 1.** Modes of life of the recorded taxa from 19 selected limestone beds, based on tiering, motility and feeding.

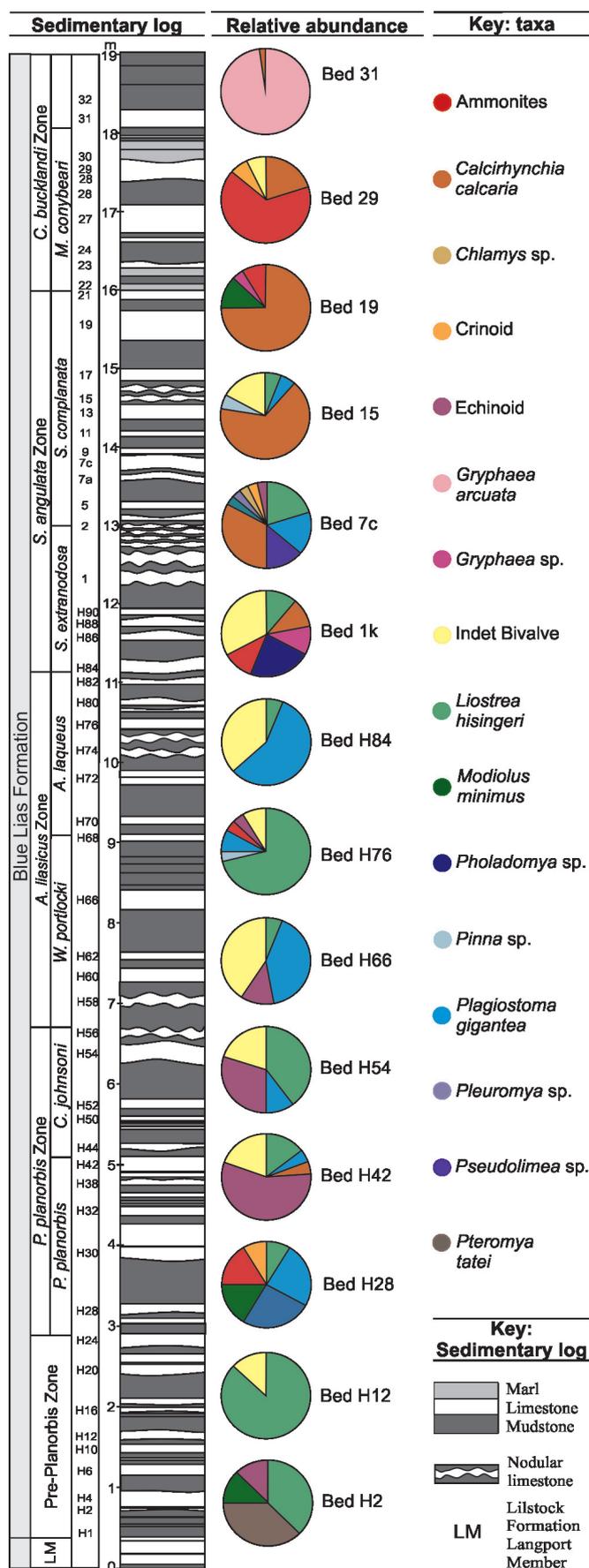


Figure 2. Relative abundances of taxa at the finest taxonomic level possible from the Pre-Planorbis Zone to the lower *C. bucklandi* Zone. The sedimentary log is numbered in accordance with Lang's (1924) scheme.

and becomes a dominant species towards the top of the *S. angulata* Zone.

A notable change occurs across the boundary between the *S. angulata* and *C. bucklandi* zones, with a return to relatively stable trends but with lower evenness and higher abundance. Within the *C. bucklandi* Zone, the maximum number of species recorded in a limestone bed drops to four. Within this zone there is a relative drop in species richness, with an accompanying increase in the dominance of ammonites (bed 29) and *Gryphaea arcuata* (bed 31). The high dominance of *Gryphaea*, with up to 51 individuals recorded within a 0.5 m<sup>2</sup> (Figure 3), is reflected within the diversity indices.

### Stratigraphic ranges and confidence intervals

The stratigraphic ranges of recorded taxa highlight invertebrate macrofaunal changes through the Blue Lias Formation. The ranges of the taxa recorded in this study have been supplemented by including occurrences from the published literature (Swift and Martill, 1999; Paul *et al.*, 2008; and the Paleobiology Database; Table 2), which extends the occurrences into the mudstone beds. This helps to reduce the biases that occur when sampling only limestone beds, because some taxa such as *Gryphaea* appear to occur more frequently in the mudstones.

Some taxa have very short stratigraphic ranges in the Blue Lias Formation and are only recorded within one ammonite zone. One example is *Pteromya tatei*, which is only recorded in this study within the Pre-Planorbis Zone (Figure 4). Other short-lived taxa, including *Chlamys*, *Pholadomya* and *Pseudolimea*, occur within the *S. angulata* Zone and are driving the significant increase in abundance of taxa within the *S. angulata* Zone (Figure 4).

Taxa with the longest stratigraphic ranges include *L. hisingeri*, *P. gigantea* and echinoids, which show similar ranges and occur relatively frequently and consistently within each zone. *Liostrea hisingeri* and echinoids are first recorded in the lower beds of the Pre-Planorbis Zone (H2, H4, H12; Figure 4) with their last recorded occurrences in the *S. angulata* Zone. *Plagiostoma gigantea* is first recorded in the *P. planorbis* Zone, and ranges up to the *C. bucklandi* Zone. Other taxa, including *Pleuromya* sp. *Modiolus minimus*, *Calcirhynchia calcaria* and crinoids, also have stratigraphic ranges that extend through most of the Blue Lias Formation, from the Pre-Planorbis or *P. planorbis* Zone to the *S. angulata* or *C. bucklandi* Zone. However, none of these taxa was recorded during the intervening *A. liasicus* Zone (Figure 4). Finally, the different species of *Gryphaea* all show similar distributional patterns, with their first occurrences close to the top of the Blue Lias Formation, in the *S. angulata* Zone, whereupon they continue to occur relatively frequently into the *C. bucklandi* Zone (Figure 4).

In order to assess whether biases in sampling may have affected these observed ranges, and in order to predict likely maximum local ranges for these taxa, confidence intervals of 80% and 95% have been constructed for the individual taxa, using the technique proposed by Marshall (2010). Some confidence intervals exceed the sampled interval, continuing below the base of the Pre-Planorbis Zone and/or above bed 35 in the Blue Lias Formation (Figure 4). For example, the lower confidence intervals for *Pleuromya* sp., *Pinna* sp., *Modiolus minimus* and crinoids extend below the base of the formation. Confidence intervals are partly a measure of the density of sampling and frequency of occurrence within the taxon's known range, and lengthy intervals suggest poorly sampled or infrequently encountered taxa. Further work should better constrain these. Confidence intervals suggest that some taxa, such as *Gryphaea*, which are very abundant towards the top of the formation, are unlikely to be found below the *P. planorbis* Zone, whereas *Pteromya tatei*, which is abundant in the Pre-Planorbis Zone, is unlikely to range higher than the *P. planorbis* Zone.

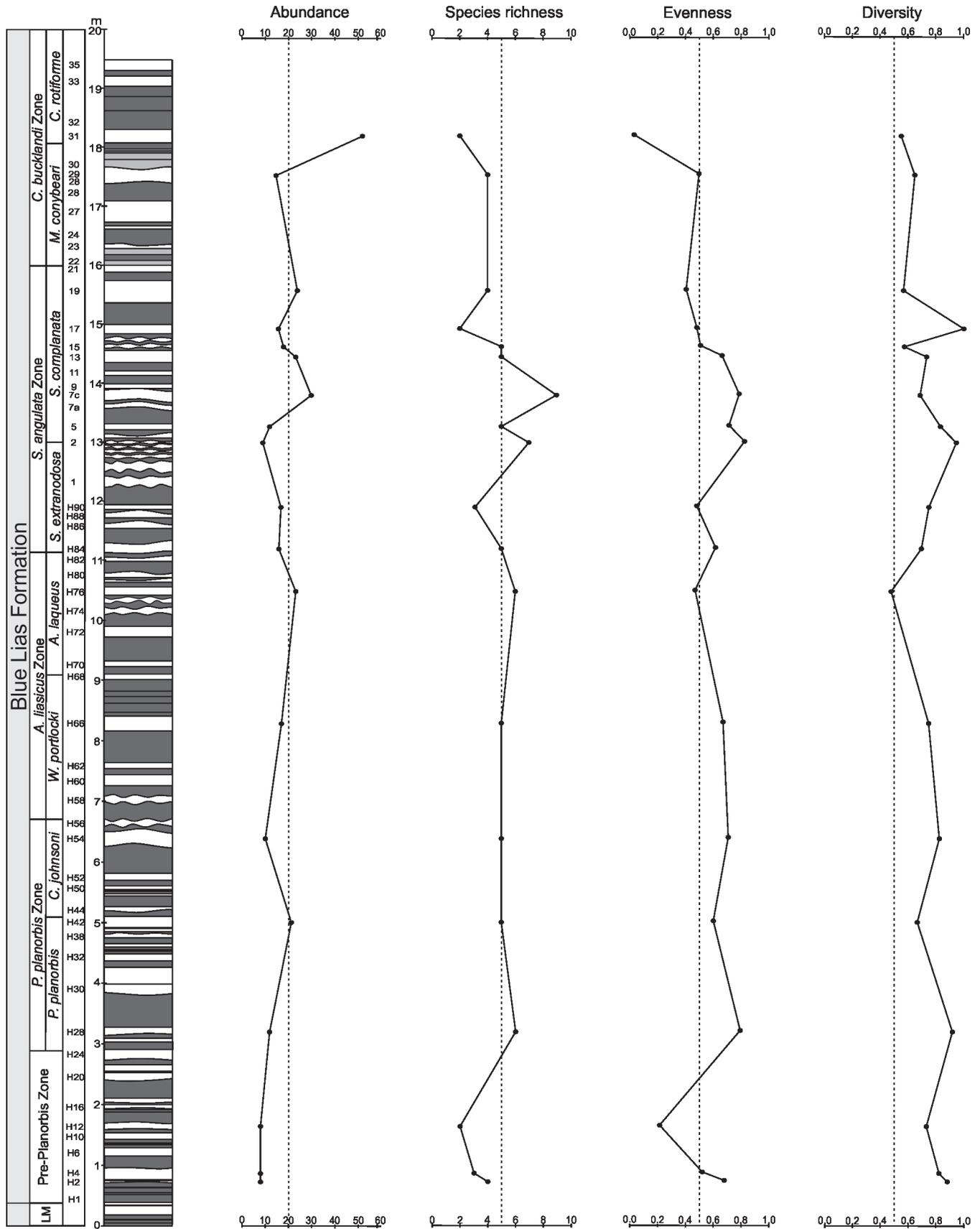


Figure 3. Palaeoecological changes through the Blue Lias Formation. Metrics are calculated from data collected from 19 limestone beds through the Blue Lias Formation and shown in Table 2.

One of the assumptions made when calculating confidence intervals is that of a constant facies or depositional environment. Although the overall range of lithofacies within the Blue Lias Formation is fairly consistent across a wide region (cf. Mander *et al.*, 2008), sedimentation rates may not have been (Jaraula *et al.*, 2013). Thus, while future work is likely to better constrain these confidence intervals, they provide a useful predictive framework of the distribution of taxa within the Blue Lias Formation at this locality given the relatively low amount of published bed-by-bed occurrence data.

### Ecospace

Due to low abundances at some horizons, samples were pooled into zones. In the Pre-Planorbis Zone, the assemblage is dominated by the non-motile, surficial suspension feeder *Liostrrea hisingeri* (Figure 5). Overall tiering levels are low, and although there are a few semi-infaunal bivalves present (*Pteromya tatei*), they only occur within two beds in this zone and there are no erect or deep burrowing taxa. Most organisms are suspension feeders, a feeding style which dominates the

Ammonite Zone		Pre-Planorbis			<i>P. planorbis</i>			<i>A. liasicus</i>	
Taxa	Bed	H2	H4	H12	H28	H42	H54	H66	H76
<i>Liostrrea hisingeri</i>		3	5	4	1	3	4	1	17
<i>Plagiostoma gigantea</i>					3	1	1	4	1
<i>Pseudolimea</i> sp.									
<i>Calcirhynchia calcaria</i>						1			
<i>Chlamys</i> sp.									
<i>Pleuromya</i> sp.									
<i>Pecten</i> sp.					3				
<i>Pinna</i> sp.									2
<i>Pteromya tatei</i>		3							
<i>Modiolus minimus</i>		1	1		2				
<i>Gryphaea obliquata</i>									
<i>Gryphaea arcuata</i>									
<i>Gryphaea</i> sp.									
<i>Pholadomya</i> sp.									
Ammonite					2				1
Crinoid					1				
Echinoid						12	3	3	1
Bivalve indet A									2
Bivalve indet B									
Bivalve indet C								3	
Bivalve indet D									
Bivalve indet E									
Bivalve indet F									
Bivalve indet G									
Bivalve indet H								1	
Bivalve indet I			2						
Bivalve indet J							1		
Bivalve indet K							1		
Bivalve indet L						4			
Bivalve indet M				1					
Bivalve indet N									
Brachiopod indet A									
Brachiopod indet B									

**Table 2.** Macrofossil abundances, as raw quadrat counts, recorded from 19 selected limestone beds. For each bed, the numbers recorded are the totals from two 50 x 50 cm quadrats, as described in the text.

Ammonite Zone		<i>S. angulata</i>									<i>C. bucklandi</i>	
Taxa	Bed	H84	H90	1k	5	7c	13	15	17	19	29	31
<i>Liostrea hisingeri</i>		1		1	3	6	2	1				
<i>Plagiostoma gigantea</i>		9	1			5	2	1				
<i>Pseudolimea</i> sp.						4						
<i>Calcirhynchia calcaria</i>				1	2	10	9	12	9	18	3	
<i>Chlamys</i> sp.						1						
<i>Pleuromya</i> sp.					1	1						
<i>Pecten</i> sp.						1						
<i>Pinna</i> sp.								1				
<i>Pteromya tatei</i>												
<i>Modiolus minimus</i>										3		
<i>Gryphaea obliquata</i>									7			
<i>Gryphaea arcuata</i>												51
<i>Gryphaea</i> sp.				1			1			1		
<i>Pholadomya</i> sp.				2								
Ammonite				1						2	10	
Crinoid						8					10	4
Echinoid						1						
Bivalve indet A												
Bivalve indet B		2										
Bivalve indet C		3	11									
Bivalve indet D		1										
Bivalve indet E			5									
Bivalve indet F					1							
Bivalve indet G					5		9	3				
Bivalve indet H												
Bivalve indet I												
Bivalve indet J												
Bivalve indet K												
Bivalve indet L				2								
Bivalve indet M												
Bivalve indet N				1								
Brachiopod indet A												
Brachiopod indet B											1	

Table 2 continued.

entire succession, but some grazing echinoids are also present (Figure 5).

The *P. planorbis* Zone records similar proportional abundances of surficial and semi-infaunal bivalves as in the previous zone, but a higher tier is also occupied with a small proportion of erect fauna, evidenced by the presence of crinoid ossicles. Within this zone, a slight shift in the most common motility style towards motile, facultative bivalves is recorded. The presence of predatory, motile, nektonic animals is first recorded in this zone due to the presence of ammonites, also observed by Paul *et al.* (2008).

The *A. liasicus* Zone is characterised by surficial, non-motile, attached suspension feeders (Figure 5). Although there is a decrease in the relative abundance of motile unattached fauna there is a slight increase in attached fauna. Suspension feeders continue to be the most common group within the feeding category accompanied by a small proportion of grazers, such as echinoids.

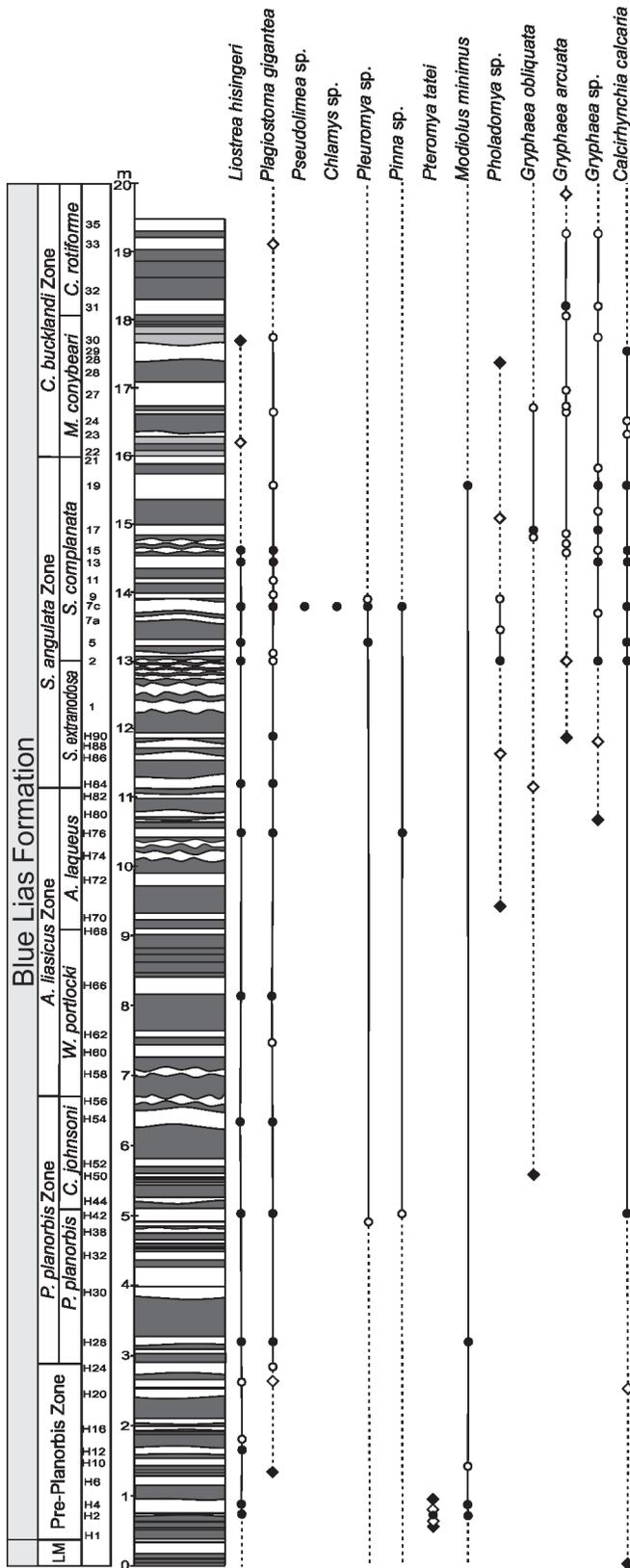
The *S. angulata* Zone records the first time in which all possible tiering groups are recorded (Figure 5). Surficial taxa dominate the tiering category, with the re-appearance of erect fauna and decrease in proportional abundance of semi-

infaunals and the first appearance of infaunals, including *Pleuromya* sp. and *Pinna* sp. (Figure 5). This is the first zone to record non-motile, unattached fauna (*Gryphaea*) whilst the relative abundances of other motility groups remain similar to the underlying *A. liasicus* Zone. Suspension feeding remains the most common feeding style, although the proportion of predators has increased substantially and grazers have declined.

In the *C. bucklandi* Zone, tiering levels are reduced once more as the semi-infaunal and infaunal taxa have disappeared. No motile bivalves are recorded within this zone and a relative high abundance of non-motile unattached bivalves is a result of a high number of *Gryphaea* present. Again, suspension feeders dominate this zone, but are accompanied by a relatively high abundance of predatory ammonites.

## DISCUSSION

The fossil assemblages found within the Blue Lias Formation of the study site are a record of the local recovery of marine communities following the Late Triassic mass extinction. Based upon characteristics such as richness, diversity, evenness, ecospace occupation and the first occurrences of key ecological



**Figure 4.** Occurrences and stratigraphic ranges, with calculated confidence intervals, of common fossil macroinvertebrate taxa recorded within the Blue Lias Formation of the study site. Occurrences recorded in this study are shown by solid circles, and published occurrences by open circles. Interpolated stratigraphic ranges are represented by continuous lines. Confidence intervals are shown by dashed lines and were calculated from all occurrence data using the methods of Marshall (2010), with the 80% and 95% confidence intervals shown by open and solid diamonds, respectively.

groups within the succession, the fossil assemblages of each of the zones have distinct palaeoecological signatures. These palaeoecological changes may reflect biotic or evolutionary changes within the fauna, or may reflect responses to changing environmental conditions associated with global climate change. Fossil assemblages may also be affected by local facies changes or sampling and rock record biases (e.g. Mander and Twitchett, 2008; Dunhill *et al.*, 2014). By focusing only on the limestone beds, using a well-defined sampling methodology, the effects of facies, sampling and rock record biases should be minimised as far as possible. In addition, there is no evidence that major geological biases, such as rock volume, have influenced the fossil record of the Blue Lias Formation of South-West England (Dunhill *et al.*, 2012). Our data should thus predominantly reflect biotic or environmental changes associated with CAMP eruptions, global climate change and the aftermath of the Late Triassic extinction event.

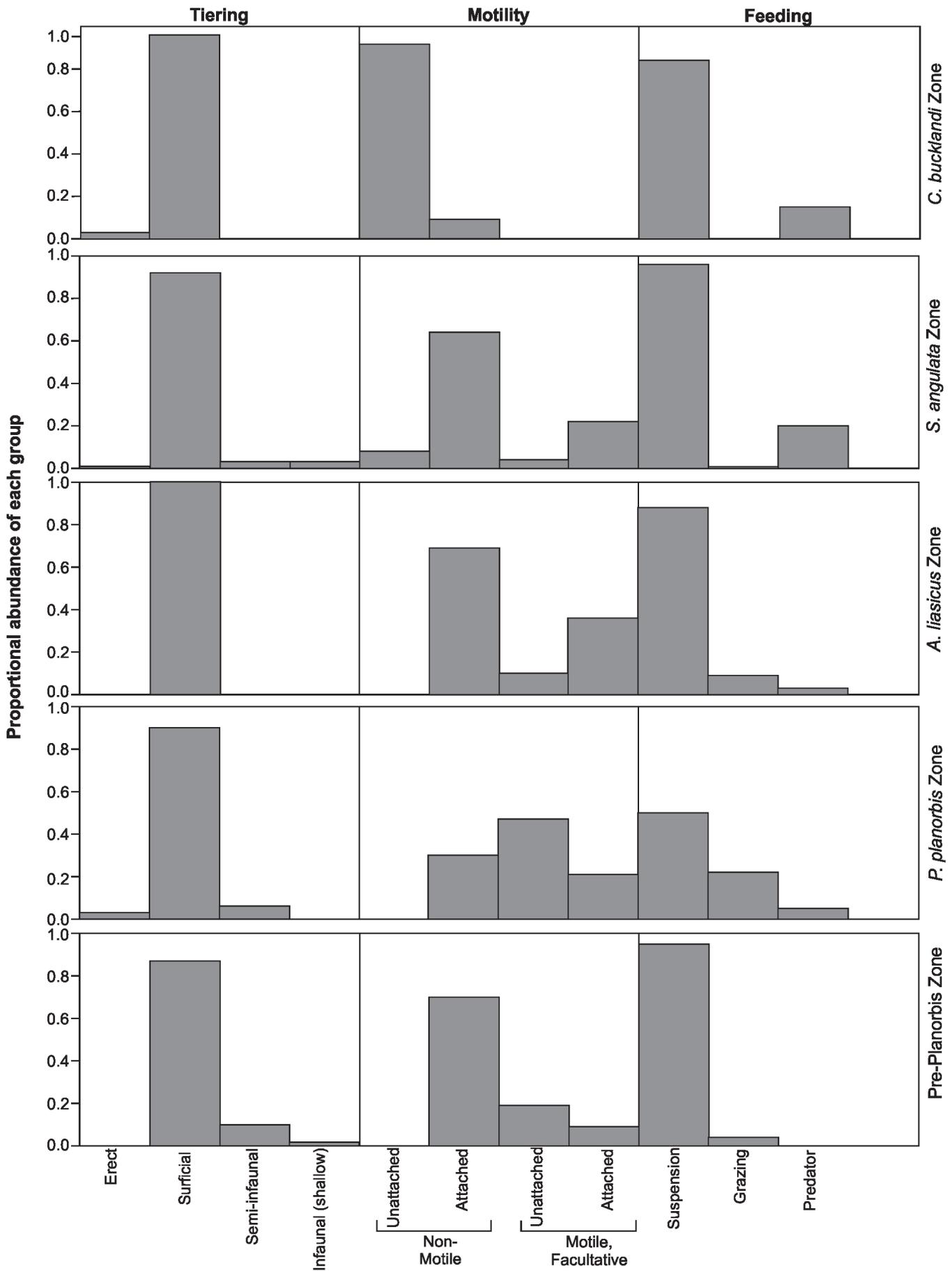
### Pre-Planorbis Beds

The lowest few metres of the Blue Lias Formation in Pinhay Bay are characterised by low abundance, richness, diversity and evenness. A reduced occupation of ecospace with an absence of high tier or deep tier organisms and relatively few ecological groups is recorded. Similar assemblages dominated by *Liostrea hisingeri* have been recorded in the basal Blue Lias Formation at Lavernock Point and at St Audrie's Bay (Mander *et al.*, 2008), and appear to be characteristic of this interval throughout the southwest UK region.

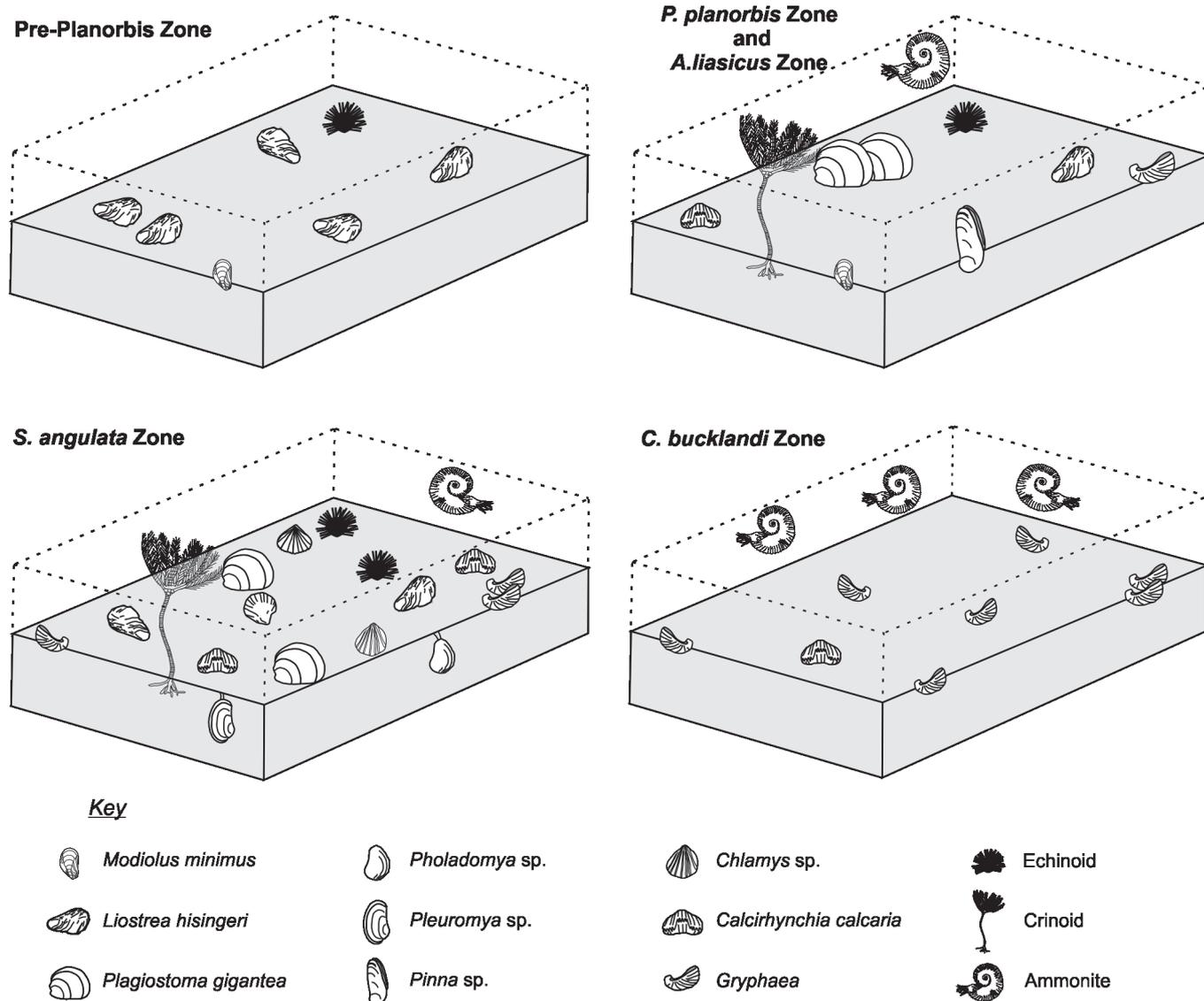
The palaeoecological characteristics share similarities with the initial, post-extinction ecosystems in the immediate aftermath of the Late Permian extinction event (e.g. Twitchett, 2006). There are many climatic and environmental similarities too (Jaraula *et al.*, 2013). The Pre-Planorbis Beds span the Rhaetian/Hettangian boundary and correlate with marine transgression, peak CO<sub>2</sub> levels and hothouse conditions following the Late Triassic extinction event (Galli *et al.*, 2005; Mander *et al.*, 2013; Jaraula *et al.*, 2013). Taxa such as *Pteromya tatei* that are confined to this short stratigraphic interval at this locality (Figure 4) and elsewhere (Warrington *et al.*, 1995) may have been especially adapted to elevated temperatures, or associated environmental changes such as frequent hypoxia. Marine fossil assemblages with similar palaeoecological characteristics may thus be common at times of peak global warming, such as in the earliest Triassic (Twitchett, 2006) and early Toarcian (Danise *et al.*, 2013). Mander *et al.* (2008) showed that the lower Pre-Planorbis Zone assemblages from St. Audrie's Bay and Lavernock Point correspond well to the post-Permian Recovery Stage 1 of Twitchett's (2006) model, but with a transition to Recovery Stage 2 in the upper Pre-Planorbis Zone with the appearance of infaunal suspension feeding burrows such as *Arenicolites*. The macrofossil data described in the present study, combined with the trace fossil data of Barras and Twitchett (2007), show that the same palaeoecological correspondence is recorded in the Pre-Planorbis Zone at Pinhay Bay too.

### *P. planorbis* and *A. liasicus* Zones

The *P. planorbis* Zone records an increase in faunal tiering (Figure 5), with the appearance of higher tiered epifaunal taxa such as crinoids. The reappearance of crinoids is considered of particular importance in the post-Permian recovery of marine ecosystems (Twitchett, 2006), and probably reflects an increase in productivity. Alongside crinoids, the co-occurrence of the ichnogenera *Rhizocorallium* and *Thalassinoides* in the *P. planorbis* Zone (Barras and Twitchett, 2007) further strengthens the similarities with Recovery Stage 3 of the Twitchett (2006) model. Through the *P. planorbis* and *A. liasicus* zones there is, however, little significant change in other palaeoecological parameters such as abundance, species richness, evenness or diversity (Figure 3). Ichnodiversity and maximum burrow depths measured from the same section in



**Figure 5.** Changes in tiering, motility and feeding strategy of the fossil macroinvertebrates of the Blue Lias Formation. Data collected from 19 limestone beds were pooled and analysed at the zonal scale. The relative proportional abundance of ecological groups with respect to tiering, motility and feeding based on number of taxa within each ammonite zone.



**Figure 6.** Sketches summarising ecological change through the Hettangian limestones of the Blue Lias Formation. See text for discussion.

Pinhay Bay also show little change through these two zones (Barras and Twitchett, 2007), and mirror the macrofossil data.

The palaeoecological data imply relatively stable, though perhaps still not optimal, palaeoenvironmental conditions during the *P. planorbis* and *A. liasicus* zones. Intervening mudstones show evidence of persistent anoxia around the base of the *P. planorbis* Zone at St. Audrie's Bay, with a weakening in the strength and duration of oxygen restriction through this interval (Jaraula *et al.*, 2013). It is likely that atmospheric CO<sub>2</sub> levels remained elevated at least through the *P. planorbis* Zone, although correlations with McElwain *et al.*'s (1999) plant beds in East Greenland are less secure in the Hettangian (Mander *et al.*, 2013).

### *S. angulata* Zone

This zone is characterised by the appearance of burrowing molluscs, such as *Pholadomya* sp., and by an overall increase in diversity and evenness. The appearance of infaunal burrowers with hard parts is mirrored by an increase in the diversity and depth of trace fossils (Barras and Twitchett, 2007). Based on their ichnological analyses, Twitchett and Barras (2004) and Barras and Twitchett (2007) concluded that the *S. angulata* Zone marked the return to normally functioning marine ecosystems after the Late Triassic extinction both locally,

regionally and globally. The palaeoecological data from this study support that conclusion, and this zone marks the first time that all possible tiering positions of the Bambach *et al.* (2007) ecospace model are occupied by fossil macroinvertebrates (Figure 5). The body and trace fossil record thus indicate that assemblages of the *S. angulata* Zone correspond to the final Recovery Stage 4 of the Twitchett (2006) model of post-extinction ecological change.

Relatively few geochemical or palaeoenvironmental studies have been published on the *S. angulata* Zone of the Blue Lias Formation, as most have focused around the Triassic/Jurassic boundary. The size, depth and diversity of the trace fossil assemblages imply a well oxygenated environment that is more optimal for benthic animals than the preceding zones. Palaeobotanical evidence indicates that atmospheric CO<sub>2</sub> levels fell back to pre-extinction values sometime within the Hettangian (McElwain *et al.*, 1999; Steinhorsdottir *et al.*, 2011), and although not well constrained biostratigraphically (Mander *et al.*, 2013) it is likely that this occurred by or during the *S. angulata* Zone.

### *C. bucklandi* Zone

Only two beds were sampled in the lower *C. bucklandi* Zone, and so the recorded changes may be an artefact of low

and selective sampling and not representative of the zone as a whole. There are some similarities with the uppermost sampled bed of the *S. angulata* Zone, and overall the beds have low richness, low diversity and, especially bed 31, high dominance (Figure 3). The assemblages record higher dominance than any other sampled bed since the Pre-Planorbis Zone, but unlike that lower zone the fossils are more abundant. The burrows from the same beds are relatively large and deeply emplaced, indicating an optimal environment for benthic animals, and, with the possible exception of the very first bed within the *C. bucklandi* Zone, are no different in size or depth than those of the *S. angulata* Zone (Barras and Twitchett, 2007).

Bed 29 is dominated by ammonites, which Paul *et al.* (2008) attributed to environmental controls such as oxygenated bottom waters and relatively slow, stable sedimentation rates with intermittent pulses of rapid sedimentation. In contrast, bed 31 is dominated by thick-shelled, calcitic *Gryphaea* (Figure 2). If this was due to preservational biases, such as the preferential loss of aragonitic taxa, then overall abundance would be expected to be low, not high (Figure 3), so it appears that as with bed 29 an environmental explanation is required. In their studies of the same section, Deconinck *et al.* (2003) demonstrated that the lower *C. bucklandi* Zone is characterised by very low kaolinite/illite ratios, which they interpret as indicating marine transgression, enhanced tectonic activity, or elevated aridity. Their data also show that the Pre-Planorbis Zone is the only other interval of the Blue Lias Formation with similarly low kaolinite/illite ratios (Deconinck *et al.*, 2003). It is perhaps no coincidence that there are palaeoecological similarities between the fossil assemblages of the *C. bucklandi* and Pre-Planorbis zones, which may reflect similar environmental controls on the local fauna, although more work is required to test this.

## CONCLUSIONS

Despite its historical importance, there have been relatively few quantitative palaeoecological studies of the fossil invertebrate macrofauna of the Blue Lias Formation at this site. The stratigraphic range chart and calculated confidence intervals (Figure 4) provide our best current estimate of the distribution of the most common taxa through the formation at this location, based primarily on quadrat studies of the limestone facies only. The fossil invertebrate macrofauna of the Blue Lias Formation, from the Pre-Planorbis Zone to the *C. bucklandi* Zone, record palaeoecological changes within a shelf ecosystem following the Late Triassic mass extinction. There is an overall change from a relatively low diversity, high dominance palaeocommunity to a high diversity palaeocommunity with a high dominance and low evenness (Figure 6). These changes are accompanied by changes in the occupation of different niches within the ecosystem, beginning with low levels of epifaunal tiering in the Pre-Planorbis Zone to higher levels of both infaunal and epifaunal tiering by the *S. angulata* Zone (Figure 6). The results of this study are similar to those of other studies of Triassic-Jurassic southwest UK sections, despite differences in methodology and types of data analysed. This study shows that Early Jurassic benthic ecosystem recovery dynamics were similar to other postulated post-extinction intervals, despite differences in the taxa involved.

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