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BODY SIZE CHANGES IN BIVALVES OF THE FAMILY LIMIDAE IN THE AFTERMATH OF THE END-TRIASSIC MASS EXTINCTION: THE BROBDINGNAG EFFECT

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Abstract: Reduced body size of organisms following mass extinctions are well-known and often ascribed to the Lilliput effect. This phenomenon is expressed as a temporary body size reduction within surviving species. Despite its wide usage the term is often loosely applied to any small post-extinction taxa. Here the size of bivalves of the family Limidae (Rafineque) prior to – and in the aftermath of – the end-Triassic mass extinction event are assessed. Of the species studied only one occurs prior to the extinction event, though is too scarce to test for the Lilliput effect. Instead, newly evolved species originate at small body sizes and undergo a within-species size increase, most dramatically demonstrated by *Plagiostoma giganteum* (Sowerby) which, over two million years, increases in size by 179%. This trend is seen in both field and museum collections. We term this within-species size increase of newly originated species in the aftermath of mass extinction, the Brobdingnag effect, after the giants that were contemporary with the Lilliputians in Swift's *Gulliver's Travels*. The size increase results from greater longevity and faster growth rates. The cause of the effect is unclear, although likely relates to improved environmental conditions. Oxygen-poor conditions in the Early Jurassic are associated with populations of smaller body size caused by elevated juvenile mortality but these are local/regional effects that do not alter the long-term, size increase. Although temperature-size relationships exist for many organisms (Temperature-Size Rule and Bergmann's Rule), the importance of this is unclear here because of a poorly known Early Jurassic temperature record.

Key words: Body size, End-Triassic mass extinction, Lilliput effect, Early Jurassic, Brobdingnag effect.

Intervals of biotic recovery, following mass extinctions, are important for the evolution of life, as new species adapt and evolve to refill ecological vacancies. Several models for biotic recovery have been proposed. Kauffmann and Erwin (1995) simply divided post extinction times into two phases: the survival interval and the recovery interval. This was later expanded by Twitchett (2006) into a four-phase process that is defined by changes in ecological tiering, species richness, evenness, bioturbation and – of relevance to this study – body size. This last factor was initially highlighted by Urbanek (1993) who documented the effects of biotic crises on the size of graptolites. He found that surviving species (those that crossed the extinction event) exhibited a reduced body size during the initial recovery phase, and later increased in size to return to "normal" pre-event body sizes; a phenomenon he termed the Lilliput effect. Urbanek's original definition was applied at the species level, however subsequent workers have loosely applied this term to a range of higher taxonomic ranks (Harries and Knorr 2009; McGowan *et al.* 2009; Huang *et al.* 2010; Sogot *et al.* 2014; Chu *et al.* 2015).

The Hettangian and Sinemurian (Early Jurassic) intervals record the recovery from the end-Triassic mass extinction (Hallam 1960, 1996; Mander *et al.* 2008; Pugh *et al.* 2014). Based on ecological tiering and trace fossil diversity, biotic recovery was considered to have been completed by the *angulata* ammonite zone, approximately 1.1 million years (Myr) after the extinction (Twitchett and Barras 2004; Barras and Twitchett 2007; Ruhl *et al.* 2010; Pugh *et al.* 2014). Hallam (1960) recorded an increase in the maximum dimensions of six bivalve species during the Hettangian and lower Sinemurian and similar trends have been noted for other bivalves and other groups at this time (Hallam 1975; 1978; 1998; Johnson 1994; Dommergues et al. 2002; Barras and Twitchett 2007). However, this is not an example of the size increase seen in Lilliput faunas returning to pre-event sizes because the species concerned were not present before the extinction event, but instead originated as small-bodied animals during the recovery. A major issue with many studies on body size changes has been a lack of species level data, with most work usually conducted at the generic level (Hallam 1975; Dommergues *et al.* 2002; Hautmann 2004) or on whole fossil assemblages regardless of their taxonomy (e.g. Mander *et al.* 2008). Such data provide little information on the mechanisms of size change and fails to distinguish intra-species size increase from manifestations of Cope's rule where evolutionary size increase occurs in a lineage (Cope 1887; Rensch 1948; Alroy 1998). An increase of average body size of a population can also record improving environments and decrease of juvenile mortality within a species or a record of changes in taxonomic composition as environments ameliorated.

Body size is a key factor in organisms because it influences ecology, physiology and evolution (e.g. Jablonski 1996). Understanding the nature and causes of body size change may reveal how animals are likely to respond to future stresses. This study aims to investigate the reported body size changes in bivalves of the British Isles during the latest Rhaetian, Hettangian and Sinemurian by considering five species of epibyssate bivalve of the family Limidae (Rafinesque): *Plagiostoma giganteum* (Sowerby), *Plagiostoma punctatum* (Sowerby), *Antiquilima succincta* (Schlotheim)*,* (Terquem)*, Pseudolimea pectinoides* (Sowerby) and *Ctenostreon philocles* (d'Orbigny)*,* with each dealt with independently to ensure taxonomic consistency. The driving mechanisms for body size change and their significance for recovery from mass extinction are discussed.

GEOLOGICAL SETTING

The upper Rhaetian of Britain consists of the Penarth Group (and its constituent Westbury and Lilstock formations). The Westbury Formation is dominated by dark mudstone beds with thin, rippled sandy horizons and densely packed shell beds (Gallois 2007). The succeeding Lilstock Formation consists of the Cotham and Langport Members. The Cotham Member is generally 2-4 m thick and formed of mudstone, siltstone and rippled, fine sandstone beds that often show an intensely deformed bed up to 2 m thick (Simms 2003). This is dissected by deep fissures, often interpreted as desiccation cracks, that can attain depths of up to 1 m (Waters and Lawrence 1987). The end-Triassic mass extinction horizon occurred near the base of this unit and was followed by the 'initial' negative carbon isotope excursion just above the crack level (Wignall and Bond 2008 and references therein).

The Langport Member exhibits the greatest lateral variation of the Rhaetian strata. In Pinhay Bay, Devon, the unit consists of micritic mudstone, giving a striking white appearance in the cliffs (hence the unit has also been known as the White Lias (Smith 1797)) and is capped by an exposure surface known as the Sun Beds (Richardson 1911). In places this bed has been cut-out and replaced by an impersistent, intraformational conglomerate (Wignall 2001). In Somerset the Langport Member, which is much thinner than along the Devonshire coast, lacks a conglomerate, instead a shaley unit termed the 'Watchet Beds' is developed in the upper part (Richardson 1911; Gallois 2009). On the Glamorgan coastline this Member is again a micritic mudstone, whilst in County Antrim this unit is characterised by shales with thin, occasionally hummocky, sandstones.

For much of the Penarth Group deposition occurred within a shallow epicontinental sea with variable connectivity to the Tethys in the south (Swift 1999). Abnormal salinity is suggested by the lack of stenohaline taxa such as ammonoids and brachiopods throughout much of the group (Hallam and El Shaarawy 1982). The presence of the ostracod *Darwinula* and the conchostracan *Euestheria* within the Cotham Member suggests brackish waters (Boomer *et al.* 1999; Morton *et al.* 2017). However, normal marine taxa such as echinoids and the ostracods *Ogmoconchella* and *Eucytherura* are present in the succeeding Langport Member (Boomer *et al*. 1999; Swift 1999).

Across southwest England and Wales the Penarth Group is overlain by the Blue Lias Formation, the base of which is marked by a black shale termed the 'Paper Shale' (Richardson 1911). The Formation consists of a rhythmic sequence of alternating limestones, marls, mudstones and dark shales thought to reflect seafloor oxygen fluctuations that were likely orbitally controlled (Weedon 1986; Bottrell and Raiswell 1989; Moghadam and Paul 2000; Wignall 2001; Clémence *et al.* 2010; Ruhl *et al.* 2010). In the Larne Basin typical offshore Blue Lias-type facies were not developed, instead the Lilstock Formation was followed by the Waterloo Mudstone Formation: a succession of pale mudstones and thin silty beds, with thin limestone beds from the upper *planorbis* Zone onwards (Simms and Jeram 2007). Also, within the Cleveland Basin the Hettangian and basal Sinemurian are represented by the Calcareous Shale Member of the Redcar Mudstone Formation, this consists of interbedded mudstones and shales with limestone beds rich in the oyster *Gryphaea* (Powell 2010). The lower Sinemurian of the East Midlands Shelf is represented by the Frodingham Ironstone Member of the Scunthorpe Mudstone Formation , the sequence here is much condensed and formed of ferruginous sandstones with chamosite ooids (Page 2004). Returning to the Southwest, the Blue Lias Formation is followed by the Charmouth Mudstone Formation, which in its lower part consists of the Shales-with-Beef and basal-most Black Ven Marls. These are distinct from the underlying Blue Lias Formation because of the greater dominance of mudstones and organic-rich shales (Gallois 2008). The Blue Lias and Charmouth Mudstone formations were deposited under fully marine conditions, with the Blue Lias representing an interval of transgression, during which the deepest waters were attained during the lowermost Sinemurian (*bucklandi* Zone) (Hallam 1981; Sheppard 2006; Sheppard *et al.* 2006). Localities on the Glamorgan coast were deposited much closer to a palaeo-shoreline than those across the Bristol Channel on the Somerset coast (Wobber 1965; Johnson and McKerrow 1995).

Despite local variations, correlation between sections is afforded by a well-constrained ammonite biostratigraphy (Bloos and Page 2002; Page 2002) except for the lowermost, ammonite-free Blue Lias. This level is known as the pre-*planorbis* beds, and is thought to be equivalent to the basal Jurassic *tilmanni* Zone (Page 2010). This is followed by the *planorbis, liasicus* and *angulata* zones of the Hettangian Stage and the *bucklandi, semicostatum* and *turneri* zones of the lowermost Sinemurian Stage.

MATERIALS AND METHODS

Species studied

The genus *Plagiostoma* has an obliquely ovate shell with length exceeding the height and is of a moderate to strong inflation. Umbones are placed posterior to the middle line and an anterior umbonal ridge is well-defined. The ligament pit is broad and the lunule excavated. The genus is edentulous or bears up to two broad, longitudinal teeth (Cox *et al.* 1969). Of the two species studied here, *Plagiostoma punctatum* is distinguished from *Plagiostoma giganteum* by the presence of approximately 100 fine radial ribs across the body of the shell and on the posterior auricle (Aberhan 1994). On abraded specimens the intersection between radial ribs and commarginal striae are rendered as punctae in the interspaces (Hodges 1987). *P. giganteum* features radial striae confined to the anterior and posterior regions of the shell, although they can be weakly developed on the centre of the valve in some specimens. Both species show a broad, flat antero-dorsal margin suggesting an epibyssate life mode and the frequent encrustation by epibionts, especially of larger specimens, further suggests an epifaunal life site.

Pseudolimea pectinoides bears an equivalved, subovate to orbicular, slightly oblique shell. The beaks are positioned centrally and are salient above the hinge line with small auricles (Cox *et al.* 1969).The shell is ornamented-by 15-20 obtuse, striated, sharp radial ribs; these may appear rounded in cross section on abraded specimens. Interspace ribs are variable in nature and can appear as sharp crests or thin rounded threads; these secondary ribs extend over the auricles (Hodges 1987; Aberhan 1994). Cox (1944) remarked how *Pseudolimea hettangiensis* was often confused with *P. pectinoides*. Further to this Cox (1944) synonymized *P. hettangiensis* and *Pseudolimea eryx*, which in turn Peter Hodges (pers. comm.) considers this to be a synonym of *P. pectinoides*.

Antiquilima succincta is obliquely subovate in outline, and only moderately inflated (Cox *et al.* 1969; Aberhan *et al.* 2011). The shell bears 30-56 primary ribs with numerous secondary ribs occupying the interspaces (Hodges 1987).

Ctenostreon philocles is distinguished by a thickened, suborbicular shell that may have a moderately irregular outline and is typically compressed. The auricles are large although the anterior auricle is usually the smaller. The surface of the shell is adorned by approximately ten rounded radial ribs that bear spines or tubercles and has broad interspaces (Hodges 1987).

Sampling

In order to document body size changes of the aforementioned bivalves across the end-Triassic extinction and throughout the Lower Lias, field collections were made from coastal locations in Somerset, Devon, Dorset, North Yorkshire, South Wales and County Antrim, a river cliff section in Gloucestershire, a quarry in North Lincolnshire and material retrieved from the Mochras borehole housed in the British Geological Survey (BGS), Keyworth, Nottingham (Fig. 1). These sections represent a range of depositional settings within the epicontinental sea that covered much of the British Isles in the Early Jurassic (Table 1). Sample horizons were distributed at 1-2 m vertical intervals, where exposure permitted. Stratigraphic height of sampled horizons was determined using published sedimentary logs (e.g. Hesselbo and Jenkyns 1995; Bloos and Page 2002; Simms 2004*a*,*b*). If no sedimentary log of sufficient resolution was available, then the section was logged either from the foreshore directly or from the corresponding cliff section and dated using ammonites.

For mudstones, shales and marls, fossils were measured and collected from freshly split surfaces by use of hammer and chisel from approximately equal volumes of rock. For the harder limestone beds, which could not easily be split, fossils were measured *in situ* from upper bedding surfaces. Samples from Hock Cliff were collected from loose blocks at the foot of the river cliff, as the section spans only a single ammonite zone these could be ascribed to the *bucklandi* Zone (Simms 2004*b*). Where bedding was exposed in ledges on river banks sampling could be undertaken *in situ* following the above described methods.

Body size data were bolstered by measurements from material previously collected housed in the School of Earth and Environment, University of Leeds, and additional specimens were donated by Michael Simms. Specimens housed in collections from the following Museums were also incorporated: National Museum of Wales, Cardiff (NMW); Warwickshire Museum, Warwick (WARMS); Bristol City Museum and Art Gallery, Bristol (BRSMG); Yorkshire Museum, York (YORYM); Whitby Museum, Whitby (WHITM); Bath Royal Literary and Scientific Institute, Bath (BRLSI).

For each specimen height (H) and length (L) of the valves were measured (Fig. 2) using a pair of digital callipers with a measurement error of +/-0.02mm. These parameters were used to calculate geometric mean body size (GMBS):$GMBS = \sqrt{(\mathrm{H\ x\ L})}$. For incomplete specimens the missing value was calculated based on H:L ratios of coeval, complete specimens. GMBS was selected for size analysis over single linear measurements as it provides a better representation of a specimen's overall size, is easily obtained and correlates well with other, more complex, body size measurements (Kosnik *et al.* 2006).

Size data were placed into time bins; ammonite zones were selected for this because they provide a high-resolution age model and allow museum specimens, with sufficient context, to be included with field observations. Durations of ammonite zones (including pre-*planorbis* beds) are from Ruhl *et al.* (2010). For the Rhaetian, which lacks ammonites, the Langport Member, Cotham Member and Westbury Formation are used as time bins, the durations of which are uncertain. Additionally, owing to small samples sizes, data from the *semicostatum* and *turneri* zones are here combined.

Size distribution histograms are produced for each time bin as well as mean GMBS along with error bars depicting a 95% confidence interval, allowing the population size ranges to be represented. Maximum body size is also shown. This is calculated as the mean of the largest 10% of the population in order to reduce the effects of abnormally large outliers (Johnson 1994). To test for statistical significance of size changes between time bins a Kolmogorov-Smirnov test (K-S test) was performed, *p*-values are quoted with a 95% significance threshold ($p < 0.05$). These analyses were carried out using PAST 3.12 statistical software (Hammer *et al.* 2001). All other analyses were carried out using Microsoft Office Excel 2013.

To test for the effects of oxygen availability on body size, specimens were divided according to their host lithology. As the sedimentary rhythms in the Blue Lias Formation are thought to represent cycles in sea-floor oxygenation, the bioturbated limestones are considered the most oxic (this category also includes the Blue Lias marginal facies – the Sutton Stone), followed by pale marl/mudstone and dark, laminated mudstone in order of decreasing oxygen availability. Size variability between locations was also assessed.

Growth lines

In order to assess changes in growth rate, spacing of growth lines was measured from well-preserved specimens using a series of overlapping, high resolution images. When compiled these give a detailed transect from the umbo to the ventral margin of the valve. Two styles of plots were produced with these data, the first plots valve height against number of growth lines, the gradient of the resulting line is taken as an indication of growth rate, and allows for statistical comparison between populations. The second plots growth line separation (mm) against growth line number. In some specimens this reveals cycles in growth line density.

External growth lines were selected over more reliable internal growth increments (Lutz and Rhoads 1980) as all of the fossils within this study are formed of recrystallized calcite or have been silicified and so lack original internal shell structures. This method is generally used in palaeontological studies (Craig and Hallam 1963; Wignall 1990; Morten and Twitchett 2009; Metcalfe *et al.* 2011) despite incurring potential errors introduced by abrasion, particularly around the umbones, and underestimation of growth lines at the clustered margins of older individuals and incorporation of disturbance lines (Craig and Hallam 1963).

RESULTS

Body size

Plagiostoma giganteum: A total of 520 specimens (including 88 museum specimens) of *Plagiostoma giganteum* were recorded from within six time bins (pre-*planorbi*s beds – *semicostatum-turneri* zones). Each of these size distribution histograms for *P. giganteum* bears a slight bimodality (Fig. 3), with the *angulata* and *bucklandi* zones showing a possible third peak. All show a slight skew towards larger individuals except for the *semicostatum-turneri* zones data that show a high proportion of small specimens (< 40 mm in size). *P. giganteum* showed an increase in mean and maximum GMBS from its first common occurrence in the *planorbis* Zone through until the *bucklandi* Zone (Fig. 4). From the *planorbis* to *liasicus* Zone mean GMBS increased by 15.6% ($p = 0.02$). The greatest relative size increase occurred between the *liasicus* and *angulata* zones (76.2% increase in GMBS, *p*=

3.95×10^{-21}). Mean body size continued to increase into the *bucklandi* Zone, however at a lessened rate (34.2% GMBS increase, $p = 1.72 \times 10^{-12}$). Altogether from the *planorbis* Zone to the *bucklandi* Zone this species increased in size by 179%. Following the *bucklandi* Zone, there were fewer occurrences of *P. giganteum,* and mean body size decreased by 74% ($p = 2.78 \times 10^{-17}$) into the *semicostatum-turneri* zones. Thus, *P. giganteum* at this level decrease to a size smaller than that seen in their earliest occurrence in the pre-*planorbis* beds even though the maximum GMBS remained high (around the size recorded from the *angulata* Zone). Bed-by-bed sampling in Pinhay Bay from the *planorbis* to *bucklandi* Zone showed an increasing body size trend that matches that of the time binned approach over the same interval (Fig. 5). The same was undertaken at Nash Point, despite the section only spanning the *angulata* and *bucklandi* zones, a trend towards a larger GMBS up-section was still seen. Throughout the studied interval minimum body size remained fairly constant around 10 mm, whereas both the mean and maximum GMBS increased up to the *bucklandi* Zone resulting in an increased size variance of *P. giganteum* populations.

Due to large samples sizes from the *angulata* Zone it is possible to test for body size differences between sampled locations (Fig. 6). *P. giganteum* specimens from Pinhay Bay and Nash Point were statistically indistinct of one another ($p = 0.27$), whilst those from East Quantoxhead were typically smaller ($p = 0.01$ and 2.00×10^{-3}, when compared to Nash Point and Pinhay Bay respectively). Testing for a link between body size and oxygenation shows that *P. giganteum* was typically larger (and more abundant) in better oxygenated settings when compared with specimens measured from dysoxic settings of the same time bin. Nonetheless, the temporal body size increase occurs within individuals from the same oxygenation regimes (Fig. 6).

Plagiostoma punctatum: This species appeared stratigraphically earlier than *Plagiostoma giganteum*, with a single specimen found in the Westbury Formation. *P. punctatum* was fairly abundant within the Langport Member (n = 27) though less common in the overlying formations with a total of 101 specimens from the six time bins (Fig 7). Of the eight time bins *P. punctatum* was recorded from, the Westbury Formation, pre-*planorbis* beds, *planorbis*, *liasicus* and *angulata* zones bore too fewer specimens to produce a meaningful histogram. The sample from the Langport Member showed a size distribution with a peak at 30 mm (Fig. 8). For the *bucklandi* and *semicostatum-turneri* zones the peak had shifted towards smaller individuals with GMBS of 10-20 mm (Fig. 8). Using the time bins with a minimum of ten specimens it is possible to see an increase in mean body size from the Langport Member to the *planorbis* Zone of 92.92% ($p = 1.67 \times 10^{-05}$). This was followed by a decline in mean GMBS from the *planorbis* to the *bucklandi* Zone of 63.9% ($p = 8.20 \times 10^{-05}$) (Fig. 7). Maximum GMBS followed the same trend as the mean. This declining trend persisted into the *semicostatum-turneri* zones with a further 25% decline in mean GMBS from the *bucklandi* Zone ($p = 8.13 \times 10^{-04}$). An additional 15 specimens were measured from BRLSI, one from YORYM and another previously collected specimen housed in the University of Leeds, these were recorded as being “Middle Lias” in age. Those from BRLSI were all collected in one location from Illminster, England. These additional specimens had a mean GMBS of 30.35 mm, a comparable value to those of the Langport Member.

Antiquilima succincta: A total of 31 specimens of *A. succincta* were assessed for this study, with this species being most abundantly recorded from the *angulata* Zone of Glamorgan. The largest specimen measured H

162.76 mm, L 161.93 mm, collected from Southam Cement Quarry, Warwickshire (WARMS G.13092). Both maximum and mean size show an increasing size trend for this species (Fig. 4). Mean size increased by 39% from the *planorbis* to the *bucklandi* Zone, although sample size is rather small. Maximum size increased by 117% over the same interval (*planorbis* to *bucklandi* Zone). This then decreased by 68% from the *bucklandi* to the *semicostatum-turneri* zones. The absolute values of maximum size for *A. succincta* were akin to, and occasionally larger than, that of *P. giganteum* (table 2).

Pseudolimea pectinoides: A total of 269 specimens from five ammonite zones (*planorbis to semicostatum-tuneri*) were measured. These revealed a mean size increase of 65% from the *planorbis* to *liasicus* Zone (p =0.03), thereafter mean GMBS remained fairly constant fluctuating slightly around 14 mm. After the *liasicus* Zone the only statistically significant size change occurred between the *bucklandi* and the *semicostatum-turneri* zones (29%, $p = 1.45 \times 10^{-03}$). Maximum size portrays a different trend, initially the *planorbis-liasicus* zone size increase was mirrored in the maximum size, however this trajectory continued (Fig. 7). Maximum GMBS shows a rise from the *planorbis* to the *bucklandi* Zone of 36% relative to the maximum during the *planorbis* Zone ($p = 3.2 \times 10^{-3}$). This size increase occurred over the same interval as that observed in *Plagiostoma giganteum* and *Antiquilima succincta*, albeit at a lesser magnitude. For all time bins, size distribution histograms show a skew in favour of smaller individuals (Fig. 9).

As *P. pectinoides* was found in a range of localities, geographic variation of body size was tested. Although few locations had data from multiple time bins (Fig. 10) a few generalisations can be made: specimens from South Wales and in the region of the Radstock and East Midlands shelves were typically larger, with the smaller specimens coming from the Cardigan Bay Basin and Co. Antrim. Further to this, as with *P. giganteum,* size differences between oxygenation regimes were also considered. This was undertaken for field observations and five samples from the marginal facies of South Wales (housed in the NMW). For all but the *liasicus* Zone the largest individuals were collected from the more aerated environments, specimens collected from sediments representing intervals of oxygen-restriction typically have GMBS around 5 mm smaller (p = 0.02). (Fig. 10). The increase in body size from the *planorbis* to the *liasicus* Zone is still recorded when comparing samples from individual oxygen regimes.

Ctenostreon philocles: Only 29 specimens of *Ctenostreon philocles* were measured from the pre-*planorbis* beds to *bucklandi* Zone. Although always scarce, this species was predominantly recorded from South Wales with a high proportion of the *liasicus* Zone specimens coming from the Sutton Stone marginal marine facies. The few specimens show only a modest maximum size increase of 15% from the pre-*planorbis* beds to the *planorbis* Zone but then remained stable between 60-64mm (Fig. 7). Mean size was equally as unvarying. The sharp increase in the *planorbis* Zone only, was not accompanied by an increased maximum size, suggesting that the *planorbis* spike was caused by an absence of small individuals. During all other time bins mean size remained around 37-41 mm. Size differences between the *liasicus* and *angulata* Zone populations were indistinct (p = 0.25) despite being from different facies (the *angulata* Zone was from typical Blue Lias offshore facies, whilst the *liasicus* Zone data come from marginal facies).

Growth patterns

Growth line analyses were undertaken only for *Plagiostoma giganteum* due to a paucity of suitably preserved material for the other species. In addition, due to the small number of suitable samples, the *angulata* and *bucklandi* zones are combined for this analysis. Specimens collected from the *planorbis* Zone had an average of 366 growth lines, this value decreased during the *liasicus* Zone with only 226 lines typically, before returning to higher values (averaging 456 growth lines) during the *angulata-bucklandi* zones. Growth rate increased from the *planorbis* to *angulata-bucklandi* zone (Fig.11), with a significant change from a mean gradient of 0.13 to 0.29 (p = 0.02) and was accompanied by an increased variability of gradients. Of the specimens from the *semicostatum-turneri* zones only one specimen was sufficiently preserved to conduct a formal growth line analyses, this had GMBS of 9.28 mm, and few, well-spaced growth lines, suggesting that this was a juvenile. *In situ* inspection of growth lines of specimens from the Charmouth Mudstone Formation confirm this. Plotting growth lines density revealed distinct patterns in a small number of specimens with up to four periods of high and low densities (e.g. from Hock Cliff (Fig. 12)). However, this growth line cyclicity was not captured in every *P. giganteum* specimen and, with the exception of a single *planorbis* Zone specimen (NMW 20.362.G18), was only encountered in the *bucklandi* Zone.

Museum versus field collections

In order to test for bias towards different size classes in museum specimens compared to those collected and measured directly from the field the two data sets were plotted separately. This evaluation was undertaken for *Plagiostoma giganteum*, owing to the larger available sample sizes. For *P. giganteum* the two collection methods show the same overall trend, with body size increasing towards the *bucklandi* Zone (Fig. 13). For the pre-*planorbis* beds there were only two specimens (one museum and one field) and so little can be said, beyond noting that they were around the same size. For the *planorbis* Zone, museum specimens contribute 24% of the data to the time bin. Specimens of this Zone collected from the field had a larger mean GMBS than their museum counterparts, although this difference is on the threshold of 95% significance (p = 0.05). For the *liasicus* Zone 30% of specimens are from museum collections, and the two collections give indistinguishable mean GMBS values. For the *angulata* and *bucklandi* zones the percentage contributed from museums decreases with only 9% and 13% of the data, for both of these time bins the data produced from the two collection styles are again indistinct ($p > 0.05$). The reversal of the size trajectory in the *semicostatum-turneri* zones was also recorded by museum specimens.

DISCUSSION

Body size

Hallam's original (1960) finding of size increase of the largest *Plagiostoma giganteum* in the first four ammonite zones of the Jurassic is replicated here. He subsequently expanded his study to include the entire Jurassic and showed that *P. giganteum*'s increase in maximum size continued into the Pliensbachian, though at a declining rate (Hallam 1975, 1998) before going extinct in the Toarcian. Size data presented here suggests this size increase was not sustained as previously reported, because the maximum body size plateaus out after a *bucklandi* Zone peak. The only other species shared between this study and those works of Hallam (1960, 1975, 1998) is *Pseudolimea pectinoides* (*Pseudolimea hettangiensis* in Hallam (1960)). Although the absolute values differ, the increased body size between the *planorbis* and *angulata* Zone reported by Hallam (1960) is confirmed in both the mean and maximum size data of this study. Our data then show mean size remained between approximately 12-14 mm from the *liasicus* Zone onwards, slightly rising in the *semicostatum-turneri* zones, whilst maximum size continued to increase into the *bucklandi* zone before reducing in the *semicostatum-turneri* zones; the same pattern observed in *P. giganteum*. Data for *Antiquilima succincta* shows that it should be added to the list of Early Jurassic molluscs that exhibited a within-species size increase. In contrast, there is no persistent size trend for *Ctenostreon philocles,* whilst *Plagiostoma punctatum* initially increases and then shows a sustained reduction in body size during the Lower Lias. Limidae size increase in the Early Jurassic is therefore impressive amongst some species but is not uniformly developed throughout the family.

Growth patterns

Specimens of *Plagiostoma giganteum* from the *angulata-bucklandi* zone achieved a larger size compared to earlier individuals for comparatively fewer growth lines. As specimens were selected for their quality of preservation, and there were no variations in the style of preservation, it is likely that this is a true biological signal. Assuming that each growth line represents the same unit of time for all specimens, then *P. giganteum* achieved an increased size through improved growth rates. These findings are consistent with those reported for *Lingula* sp. (Metcalfe *et al.* 2011) and *Pseudomytiloides dubius* (Morten and Twitchett 2009) in the wake of the Permo-Triassic and early Toarcian mass extinction events respectively; diminutive forms display a greater density of growth lines compared to larger, later forms. A similar finding has also been reported for *Pholadomya ambigua, Cardinia concinna* (Hallam 1963) and species of *Gryphaea* (Johnson 1994) in the Early Jurassic.

The high growth line counts during the *planorbis* Zone may reflect the addition of disturbance rings formed during intervals of environmental stress or spawning (Craig and Hallam 1963; Lutz 1976; Lutz and Rhoads 1980). Therefore the populations of smaller body size and higher densities of growth lines may be stunted forms indicating growth under a highly stressed environment (Metcalfe *et al.* 2011). Specimens of *P. giganteum* from the *bucklandi* Zone of Hock Cliff, record clear cycles of expanded and contracted growth, this may indicate that these specimens lived in a stable, low stress environment and therefore have fewer disturbance rings masking a regular growth pattern, which may be annual. The greater number of growth lines on the largest individuals from the *angulata-bucklandi* zone may therefore reflect increased longevity, and so the gigantism was achieved through both greater growth rates and a longer life span.

Contemporary Early Jurassic size increases

Early Jurassic size changes were not restricted to the Limidae, Hallam (1960, 1975) reported size increases for three epifaunal, two semi-infaunal and two infaunal suspension feeding bivalve species and for the nautiloid *Cenoceras striatus*. For *Liostrea irregularis and Cardinia concinna* this size increase persisted until the Pliensbachain. A similar case was noted for the pectinid *Chlamys textoria* with a size increase persisting through until Pliensbachian stage (Nürnberg *et al.* 2012). During the same interval that *Plagiostoma giganteum* increases in size (*planorbis* to *bucklandi* Zone) there is a marked increase in the size of ammonites. However, this was a rapidly evolving group and the size increase occurs amongst successive species; this is a good example of Cope's Rule (Hallam 1960; Dommergues *et al.* 2002). In contrast, the trends shown here occur within species and is not an evolutionary trend but an ecophenotypic response.

Causes of body size and growth rate changes

Water depth and body size. Water depth is thought to exert a control over body size due to variation of factors such as availability of food and oxygen (Shirayama 1983; Peck and Harper 2010; Shi *et al.* 2016). Several studies have shown that body size can decrease with depth (e.g. Attrill *et al.* 1990; Olabarria and Thurston 2003; Kaariainen and Bett 2006; Shi *et al.* 2016). This was shown by the *Plagiostoma giganteum* data with the populations in the offshore East Quantoxhead location having a smaller mean body size than the contemporaneous specimens from the shallower Nash Point and Pinhay Bay sites. For *Pseudolimea pectinoides* the same pattern was not as clear although the largest individuals were recorded as being from the comparatively shallow shelf settings. Despite these observations, water depth does not explain the temporal pattern of body size increase in *P. giganteum* in the Blue Lias Formation because it was deposited during an overall deepening trend (Hallam 1981; Sheppard 2006; Sheppard *et al.* 2006). The initially small size of *Plagiostoma punctatum* in the Langport Member may relate to the reported unusual salinity at this level (Hallam 1965; Hallam and El Shaarawy 1982), but this is unlikely to be an influencing factor for the other species because they first appear above the Langport Member.

Oxygen availability. Oxygen restriction is generally regarded as a cause of reduced body size in marine invertebrates (Rhoads and Morse 1971; Richmond *et al.* 2006). Under low oxygen levels metabolic rates are reduced, and growth slowed (Richmond *et al.* 2006). Anoxic and euxinic conditions did develop intermittently during the lowermost Jurassic in our study area and are manifest as black shales and laminated limestones (Hallam 1987; Wignall and Hallam 1991; Wignall 2001; Richoz *et al.* 2012). These facies are best developed in the earliest Jurassic and typically become less frequent in the *angulata* and *bucklandi* zones, suggesting overall improved benthic oxygenation (Wignall and Hallam 1991). This trend occurred in tandem with the increased body size seen in the Limidae species. Greater oxygen restriction in the more offshore/deeper sections seen in the upper Hettangian and Sinemurian of north Somerset may explain the smaller size of *P. giganteum* from that section.

The larger mean body sizes of both *Plagiostoma giganteum* and *Pseudolimea pectinoides* were found in bioturbated limestone and pale marls compared to the darker lithologies. Furthermore, *P. giganteum* is only common in the bioturbated limestones of the Blue Lias Formation further indicating its preference for better oxygenated conditions. These observations clearly indicate a link between body size and oxygen but they fail to account for the long-term trend of size increase because *P. giganteum* exhibits within-lithology (and therefore oxygen regime) size increases over the first 2 million years of the Jurassic.

The trend of size increase for the species of *Plagiostoma giganteum* and *Antiquilima succincta* was reversed in the *semicostatum-tuneri* zones. Most of the data for this interval comes from the Charmouth Mudstone Formation of the Wessex Basin. The lower two members of this unit (Shales-with-Beef and Black Ven Marl members) are dominated by black shales with benthos restricted to thin discrete beds that likely record brief oxygenated intervals superimposed on a background of intense anoxia (Wignall and Hallam 1991). Inspection of valves revealed a low number of widely spaced growth lines indicating the small specimens were juveniles and not stunted adults. This is corroborated by the size-frequency histograms that show a left-skewed distribution (Figs 3). The small sizes of individuals in the *semicostatum-turneri* zones is thus not comparable to the small sized specimens of the *planorbis* Zone but instead a local response to harsh conditions. This is corroborated by the continued presence of large, contemporary individuals of *P. giganteum* from the Bristol Channel Basin and from the East Midland Shelf which attain sizes as great as 170 mm. The same is true for specimens of *Pseudolimea pectinoides*. Thus, the size increase trend was locally reversed by regional anoxia but without affecting the overall trajectory.

Temperature and Body Size. The relationship between temperature and body size has been extensively studied for a wide range of organisms (McNab 1971; Geist 1987; James *et al.* 1995; van Der Have and De Jong 1996; van Voorhies 1996; Atkinson and Sibly 1997; Mousseau 1997; Roy and Martien 2001; Schmidt *et al.* 2004; Linse *et al.* 2006; Arendt 2011; Berke *et al.* 2013). Perhaps the most renowned temperature-related size rule is Bergmann's rule (Bergmann 1847; translated in James 1970) whereby an organism's body size increases with latitude. Although Bergmann's rule specifically refers to geographic body size distribution, it is thought to relate to the temperature-size rule which relates solely to the effects of temperature on growth and final adult body size (Atkinson 1994; van Der Have and De Jong 1996; Atkinson and Sibly 1997). Generally growth and development rates increase with temperature thereby shortening the time taken to reach maturity and producing a small adult (Atkinson 1994; Kingsolver and Huey 2008; Chown and Gaston 2010).

The role of temperature in the size increase of the early Jurassic Limidae is difficult to evaluate because of a poorly constrained temperature record. The end-Triassic mass extinction interval is thought to have been a period of intense warming, with fossil leaf stomatal indices suggesting a temperature increase of around 3-4°C (McElwain *et al.* 1999). The subsequent climatic cooling is not well constrained although it may have occurred during the *planorbis* Zone (McElwain *et al.* 1999; Bonis 2010; Mander *et al.* 2013). Study of British sections instead suggests a warming trending (derived from oxygen isotope ratios of *Liostrea* shells), from <7-14°C in the

Langport Member to 12-22°C in the *planorbis* Zone (van de Schootbrugge *et al.* 2007; Korte *et al.* 2009; Clémence *et al.* 2010). However, the salinity of the Langport Member is unlikely to have been normal marine (Hesselbo and Jenkyns 1995; Wignall 2001; Radley *et al.* 2008), making evaluation of the isotope record difficult. Clay composition provides an indirect indicator of palaeoclimate with high kaolinite/illite ratios thought to indicate wetter and possibly warmer climatic episodes (Deconinck *et al.* 2003). If so, data from SW England suggests the *planorbis* and upper *bucklandi* zones may have been warm and humid intervals with the *liasicus* and *angulata* zones being cooler and drier (Deconinck *et al.* 2003). The clay mineral changes (and the oxygen isotope data) do not appear to relate to the long-term size increase of the Limidae and therefore suggest that the trend is not an example of the temperature-size rule. However, there is a clear need for a more reliable palaeotemperature curve for Early Jurassic time to better assess any size-temperature link.

Food availability.

Changes to primary productivity can influence body size and growth rate of organisms higher in the food chain (Hallam 1965; Epifanio 1979; Wacker and von Elert 2008; He *et al.* 2010; Brom *et al.* 2015) and may have played a role in the initially small size of bivalves after the end-Triassic mass extinction. A productivity crash has been postulated for this crisis (Ward *et al.* 2004; Bottini *et al.* 2016) resulting in unusual Early Jurassic marine primary productivity with larger red algae (dinoflagellates) replaced by smaller green algae: prasinophytes and acritarchs (van de Schootbrugge *et al.* 2007) and occasionally cyanobacteria (Jaraula *et al.* 2013). Such communities prevailed during pre-*planorbis* to lower *planorbis* Zone interval only (van de Schootbrugge *et al.* 2007; Clémence *et al.* 2010; Paris *et al.* 2010) and may account for the small body size of bivalves (relative to later during the recovery). The smaller size of acritarchs and prasinophytes (relative to the dinoflagellates) could cause reduced efficiency of filtration in suspension-feeding bivalves (Weiss *et al.* 2007; van de Schootbrugge and Gollner 2013). Whilst prasinophytes and cyanobacteria lack essential long-chained polyunsaturated fatty acids that are required for growth (Brown *et al.* 1997; von Elert *et al.* 2003): both factors could reduce growth rates. However, such notions are speculative and difficult to disentangle from other co-occurring stresses.

Lilliputians and Brobdingnagians

The Lilliput effect is defined as a temporary reduction in body size of a surviving species after a biotic crisis (Urbanek 1993), and is not applicable to the small-sized individuals of *Plagiostoma giganteum, Antiquilima succincta* and *Pseudolimea pectinoides* seen in the aftermath of the end-Triassic mass extinction, because these species are first recorded at this time. Their trend is one of within-species size increase following first appearance. We propose to name this as the Brobdingnag effect (after the land inhabited by giant humans in Swift's *Gulliver's Travels*). We do not view this as a manifestation of Cope's rule which involves the evolution of progressively larger species which includes an accompanying morphological change (Rensch 1948). Were this change in body size to be viewed as Cope's rule with species succession occurring as an anagenetic change we would be required to erect a new species name for the larger bivalves in the *angulata* and *bucklandi* zones. As size alone distinguishes the younger populations with no other morphological change we feel this to be inappropriate.

For the Limidae examples, the size increase is caused by increased growth rates and greater longevity of individuals suggesting improving benthic conditions were responsible. These could include improved oxygenation, because populations of smaller body size (caused by higher juvenile mortality) are found in areas experiencing frequent anoxic conditions. There may be a temperature-size relationship but this is difficult to judge without a reliable palaeotemperature curve. However, the cause of the overall, long-term trend (spread over 2 million years) is unclear as not all species show a dramatic size.

Both the Lilliput and Brobdingnag effects relate to the observation that small species commonly dominate in the immediate aftermath of extinction intervals. There have been several explanations for the former effect. Payne (2005) suggested four models that could have produced assemblages of small gastropods in the aftermath of the Permo-Triassic mass extinction (although he did not explicitly call any of these alternatives the Lilliput effect): 1) *size-biased extinctions* (preferential extinction of large taxa); 2) *changed relative abundances* (increased relative abundances and dominance of small taxa thereby lowering the mean size of an assemblage); 3) *size change within-lineages* (evolutionary trend towards smaller species via anagenesis); 4) *size-biased originations* (origination of new species in the aftermath of the extinction that were preferentially small). Twitchett (2007) later considered model 3 to be the Lilliput effect (although this does not fit the original definition which was a within-species size decrease). As Harries and Knorr (2009) noted, model 3 is an example of the concept of dwarfing, as defined in Marshall and Corruccini (1978), although frequently it also involves speciation. We ascribe Payne's model 4 to the Brobdingnag effect with the modification that species increase in size following their appearance.

The term "Lilliput effect" has been widely used but often applied at a higher taxonomic rank than species and so we suspect that many, perhaps the majority of examples, are in fact manifestations of the Brobdingnag effect. Many studies of the supposed Lilliput effect lack size data showing a return to pre-extinction sizes (e.g. Kaljo 1996; Keller and Abramovich 2009; Huang *et al.* 2010; Song *et al.* 2011; Martínez-Díaz *et al.* 2016; Belben *et al.* 2017), or the taxonomic rank is often generic or higher (e.g. Borths and Ausich 2011; Chen *et al.* 2013; Chu *et al.* 2015; Weronika *et al.* 2017), or it is applied to whole assemblages irrespective of taxonomy (Mander *et al.* 2008; Belben *et al.* 2017). Under such circumstances it may not be possible to detect if individual species crossed the extinction event, exhibit a reduced body size in the aftermath and then increased in size during the recovery, as per the Lilliput effect. Alternatively, a surviving genus could be represented by new species with small bodies that then undergo a within-species size increase, as per the Brobdingnag effect. These can only be tested with more studies conducted at the species level and for the entire recovery interval. One such study (Chen *et al.* 2018) testing for the Lilliput effect in brachiopods following the end-Permian mass extinction shows that species originating in the aftermath did so with small body sizes and subsequently increased in size, thus following a Brobdingnag trend. Additionally Morten and Twitchett (2009) showed that, what is here termed the Brobdingnag effect, occurred amongst three species following the early Toarcian mass extinction event (*Acrocoelites subtriscissus, Melegrinella substriata, Gresslya donaciformis*). With an increase in studies conducted at the species level it may be found that the Brobdingnag effect was more prevalent through geological time than the Lilliput effect.

CONCLUSIONS

Three species of Limidae (*Plagiostoma giganteum, Antiquilima succincta* and *Pseudolimea* pectinoides) show increased body size during the first 2 million years of the Jurassic following the end-Triassic mass extinction. Of these *P. giganteum* is the most impressive case with a substantial increase in mean shell size (179%) from the *planorbis* to the *bucklandi* Zone. The larger specimens of *P. giganteum* from the *bucklandi* interval show an increase in the number and spacing of growth lines when compared to those from earlier times, indicating larger size was achieved by faster growth and greater longevity. We proposed that this within-species size increase in the aftermath of a mass extinction be termed the Brobdingnag effect and argue that many so-called example of the Lilliput effect (reduction in size of species across a mass extinction horizon) need to be re-evaluated. They may represent the origination of small, new species followed by subsequent size increase. The Brobdingnag effect was not ubiquitous within the Early Jurassic Limidae though, because *Ctenostreon philocles* did not undergo significant size changes and *Plagiostoma punctatum* decreased in size.

The cause of the Brobdingnag effect is unclear. There is apparently no connection with temperature fluctuations although a paucity of reliable Early Jurassic temperature records makes this factor difficult to evaluate. Oxygen-poor conditions clearly caused Limidae populations to become smaller in body size, because of increased juvenile mortality, but this is a local/regional effect and does not influence the long-term size-increase trend. It remains a remarkable finding that some bivalves are capable of substantial changes in size that presumably involved changes in ecological style, whilst remaining a morphologically distinct species.

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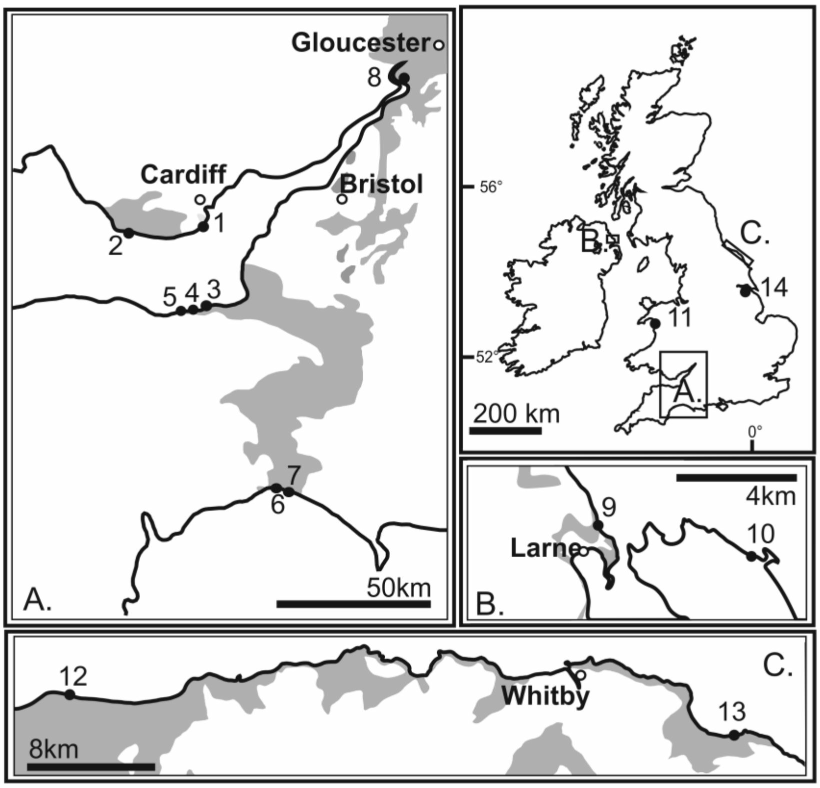

Figure 1. Map depicting field locations (closed circles), see Table 1 for details, shaded regions depicting Rhaetian and Early Jurassic outcrops. Maps modified from Mander et al. (2008) and Powell (2010).

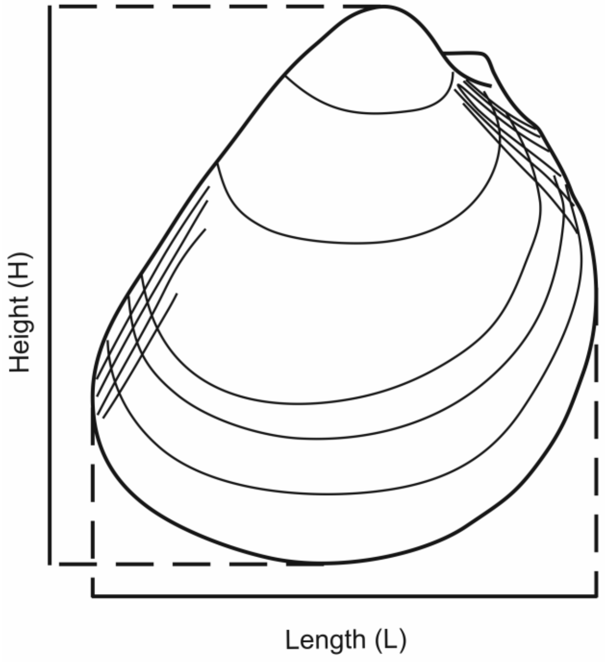

Figure 2. Measurement schematic of a left valve in Limidae.

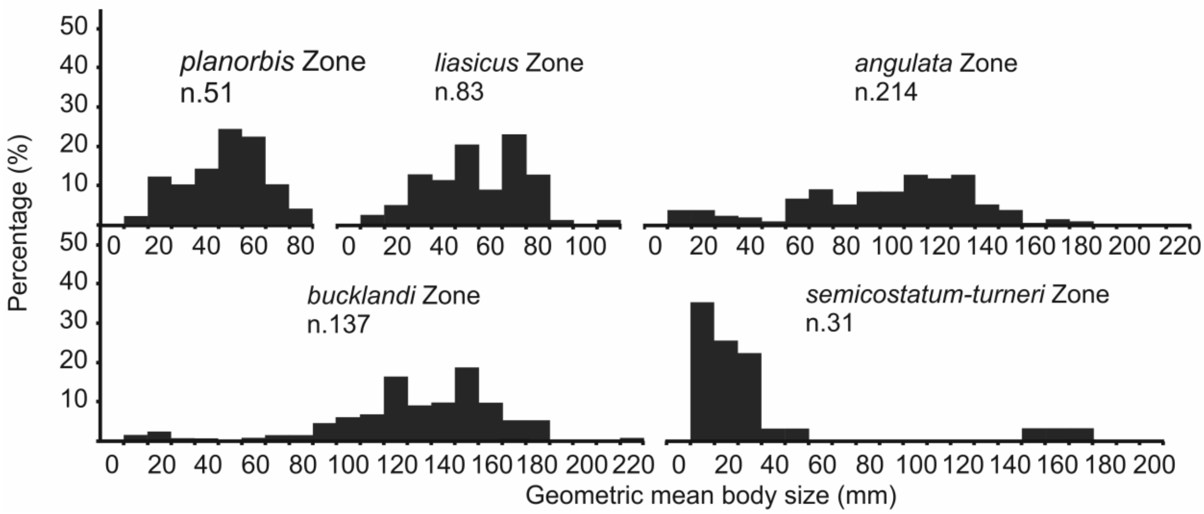

Figure 3. Size distribution histograms for Plagiostoma giganteum per time bin.

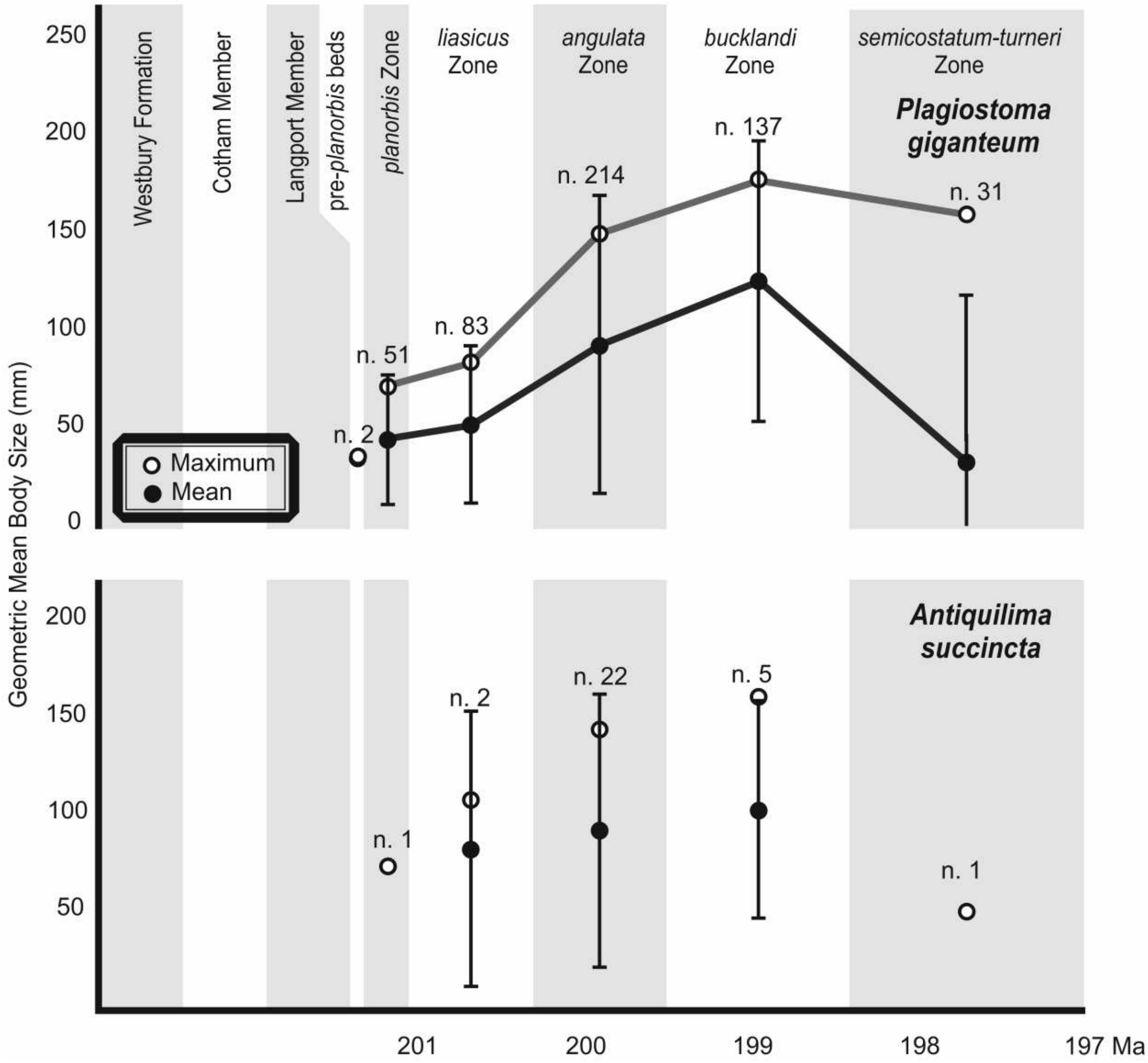

Figure 4. Time-binned variation in the size of Plagiostoma giganteum (top) and Antiquilima succincta (bottom). Lines connect successive time bins with >10 specimens. Error bars depict 95% confidence intervals. Sample size quoted per time bin.

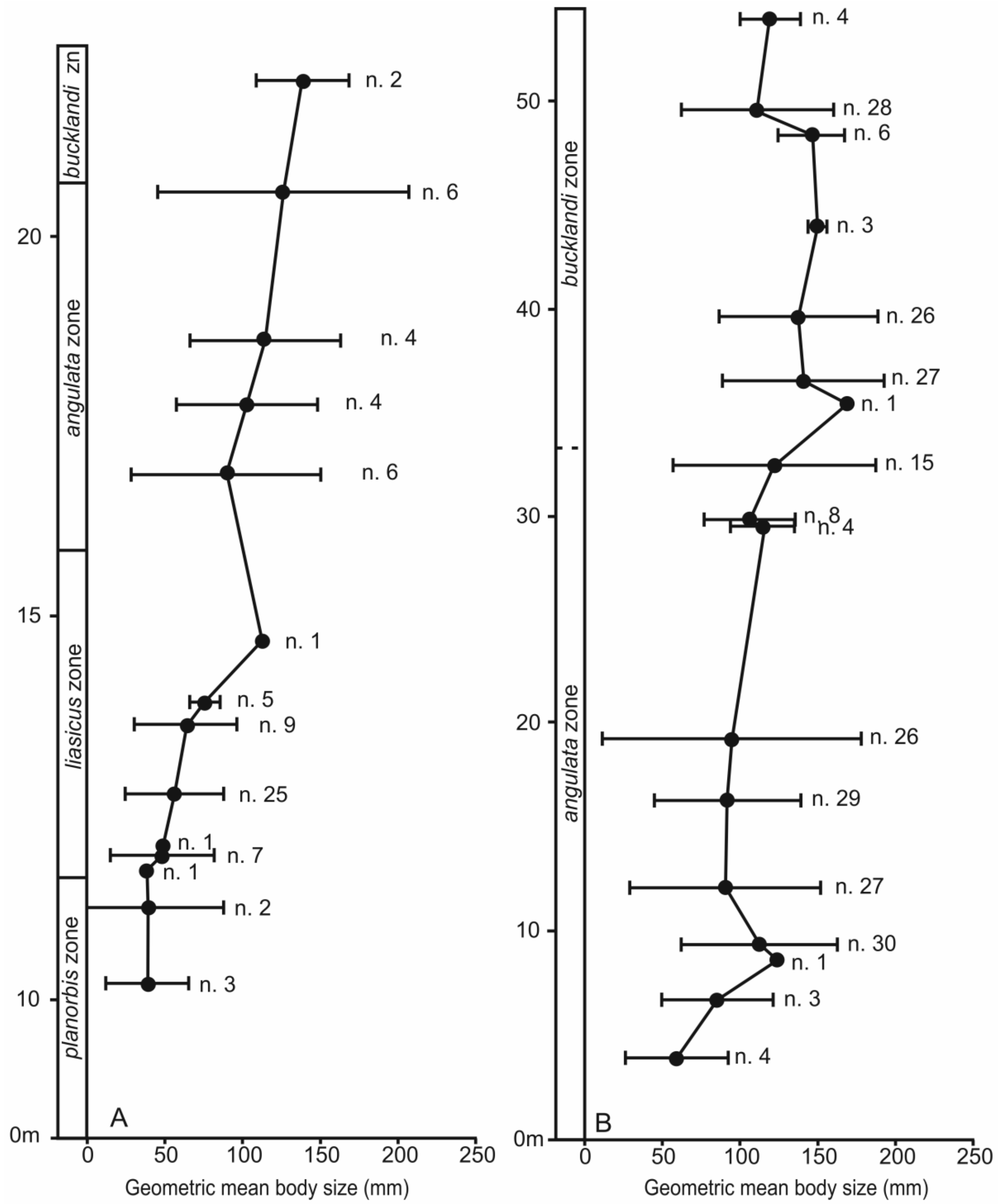

Figure 5. Stratigraphically tied size variation of P. giganteum from Pinhay Bay (A) and Nash Point (B). Error bars depict 95% confidence intervals. Note different vertical scales.

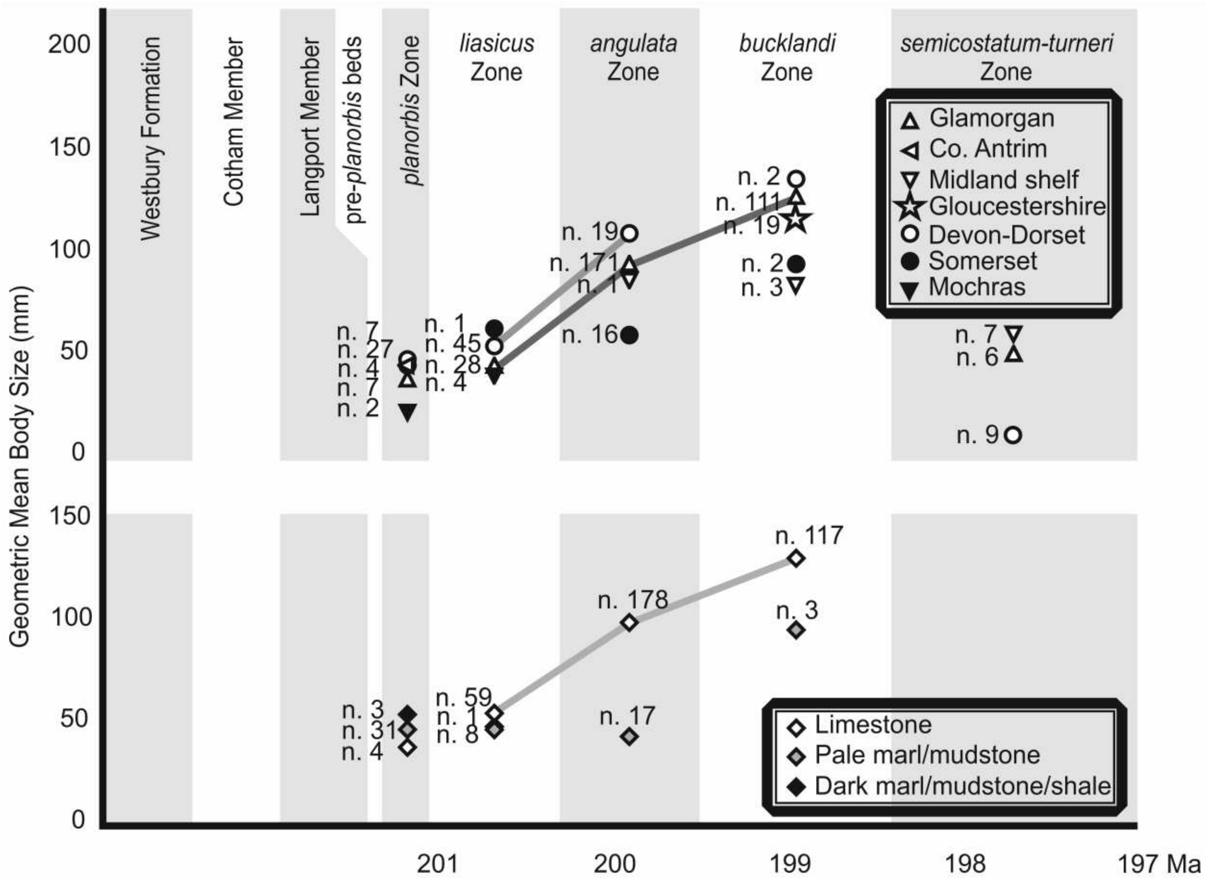

Figure 6. Time-binned variation in the size of Plagiostoma giganteum per locality, (top). Variation in size between specimens measured from different oxygenation regimes inferred from host lithology, see methods for details. Lines connect successive time bins with >10 specimens. Sample size quoted per time bin.

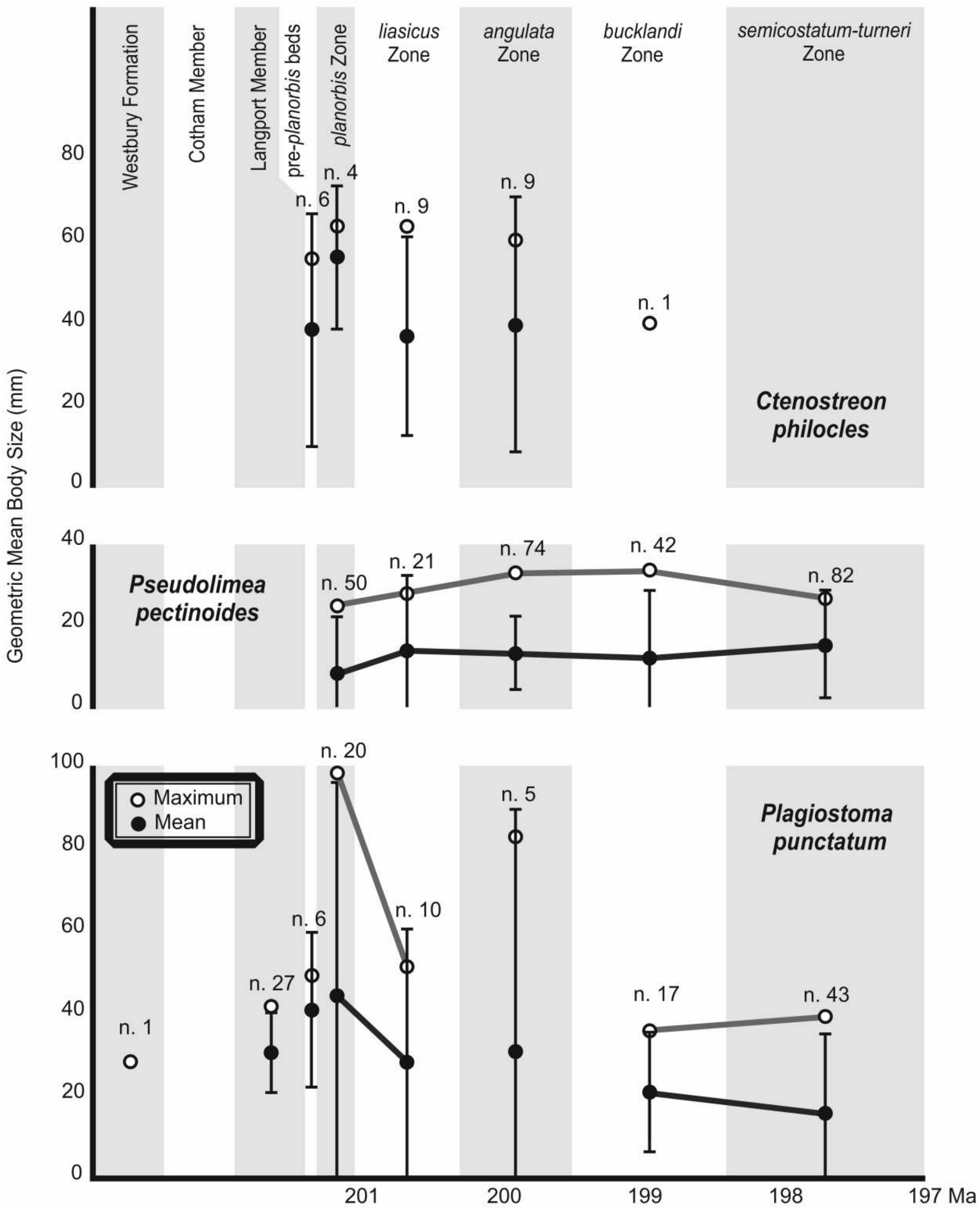

Figure 7. Time-binned variation in the size of Ctenostreon philocles (top), Pseudolimea pectinoides (middle) and Plagiostoma punctatum (bottom). Lines connect successive time bins with >10 specimens. Error bars depict 95% confidence intervals. Sample size quoted per time bin.

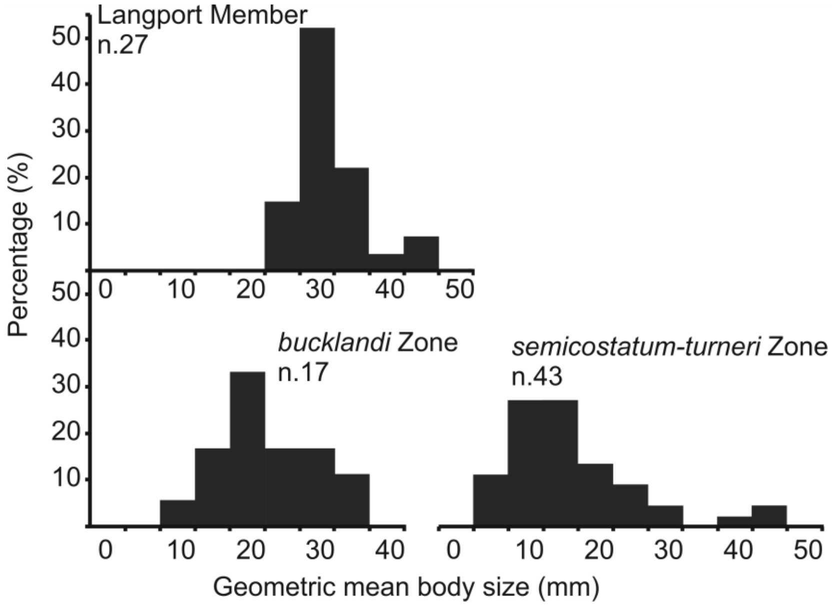

Figure 8. Size distribution histograms for Plagiostoma punctatum per time bin with sufficient samples.

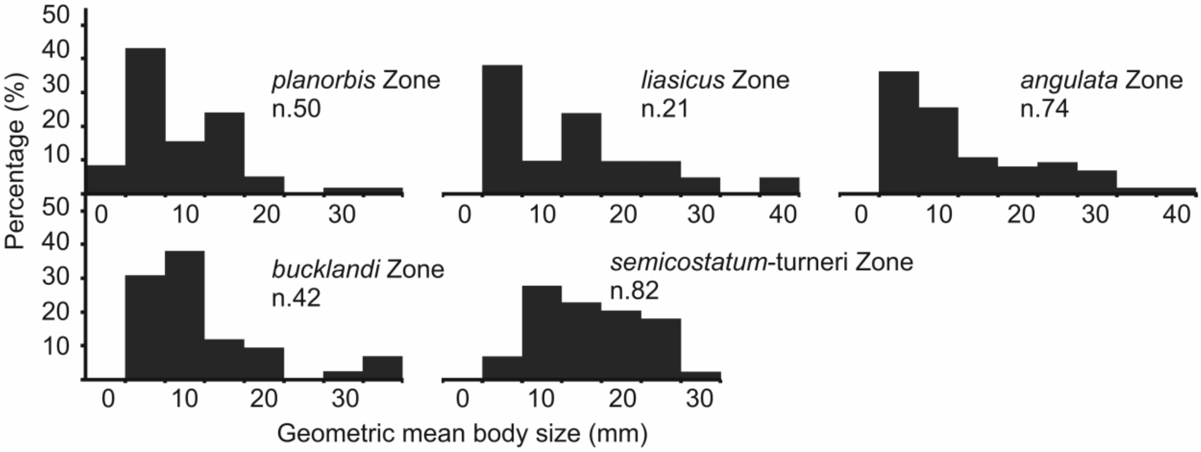

Figure 9. Size distribution histograms for Pseudolimea pectinoides per ammonite zone.

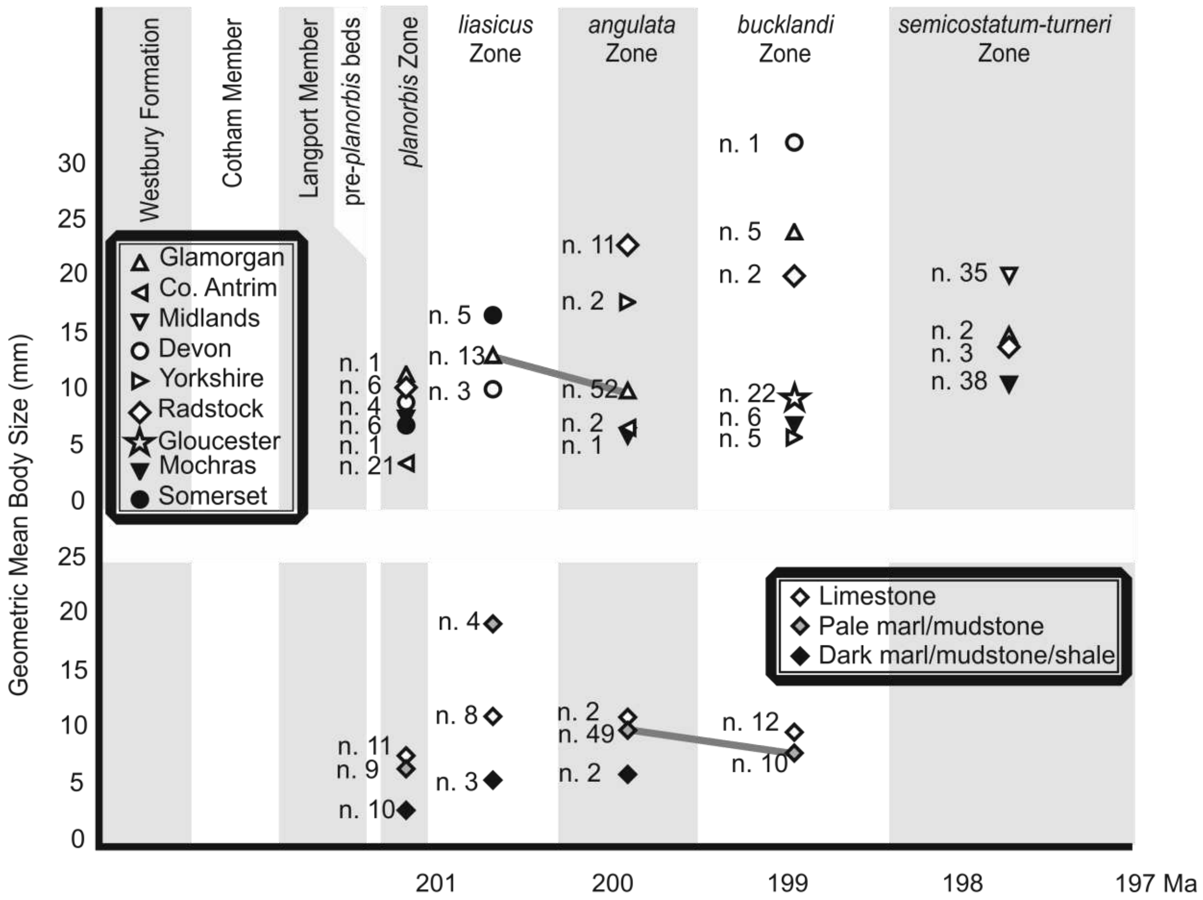

Figure 10. Time-binned variation in the size of Pseudolimea pectinoides per locality, (top). Variation in size between specimens from different oxygenation regimes inferred from host lithology, see methods for details. Lines connect successive time bins with >10 specimens. Sample size quoted per time bin.

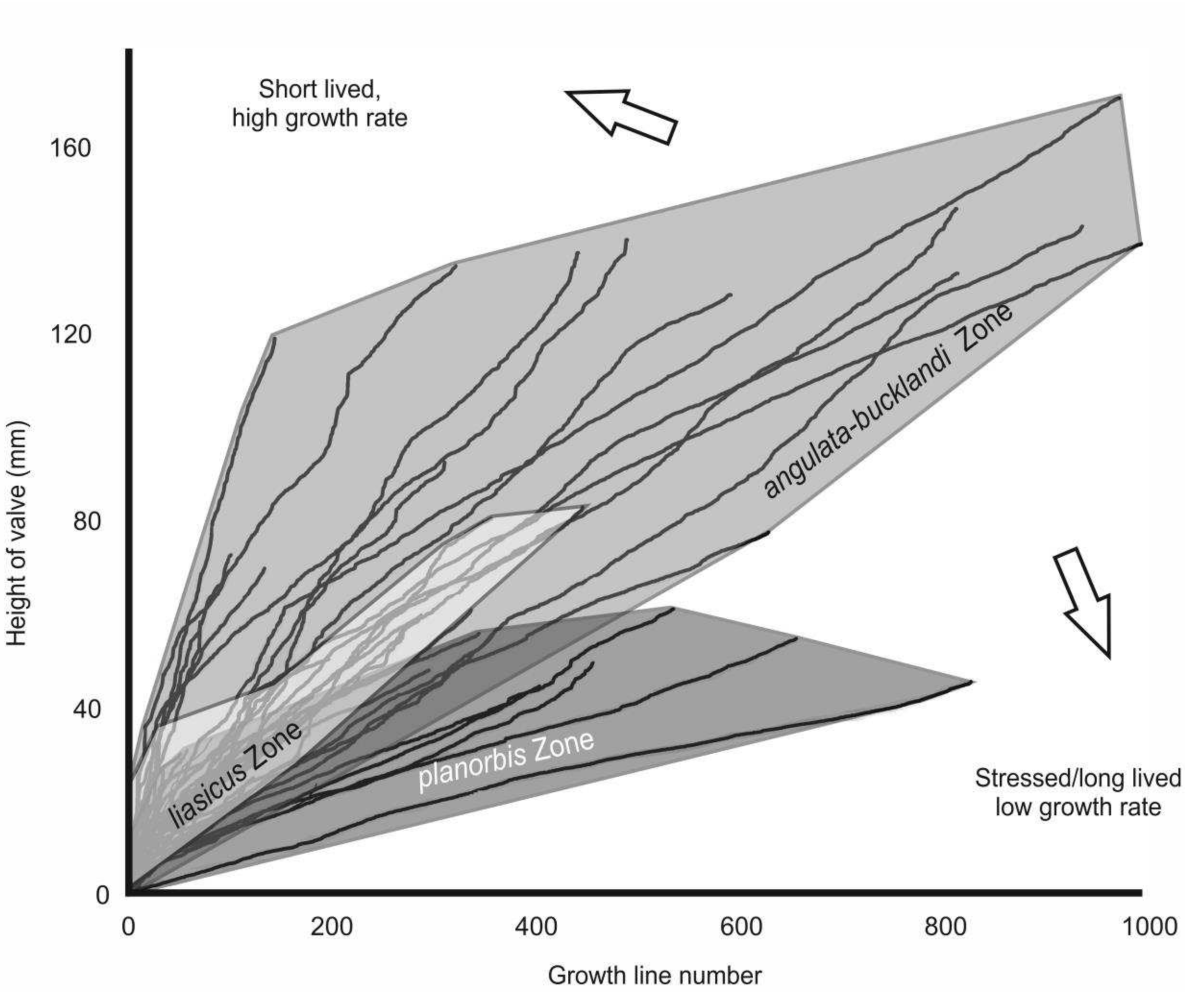

Figure 11. Growth rate plot for Plagiostoma giganteum. Individual lines depict growth trajectories of single specimens. Shaded regions define spread of data per time bin.

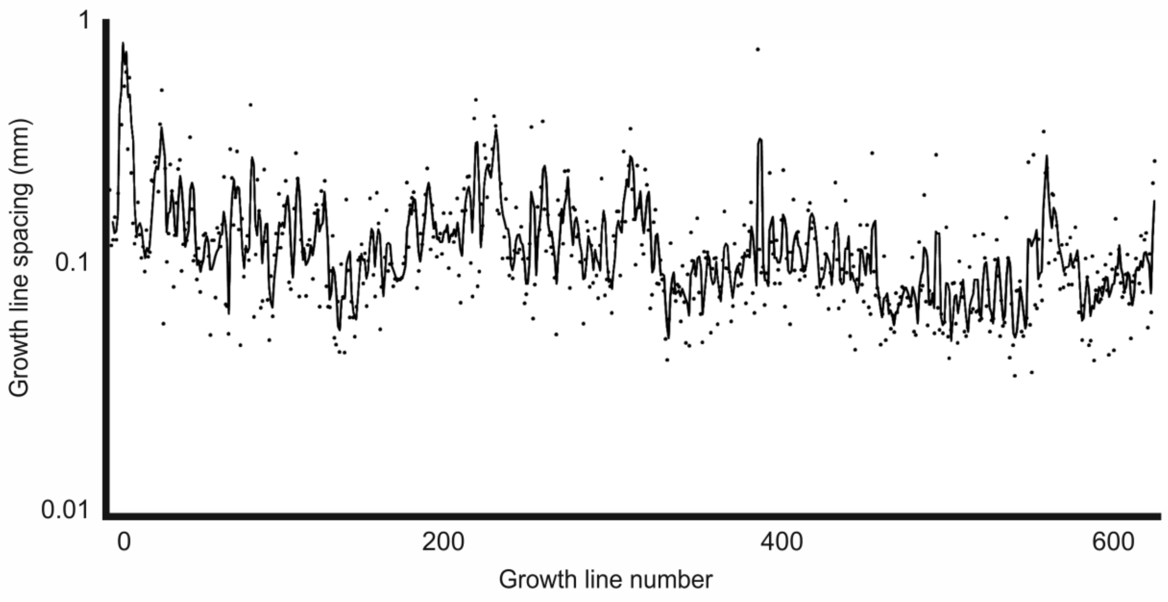

Figure 12. Growth line densities with a three point moving average trend line showing cycles in a large Plagiostoma giganteum collected from the bucklandi Zone of Hock Cliff.

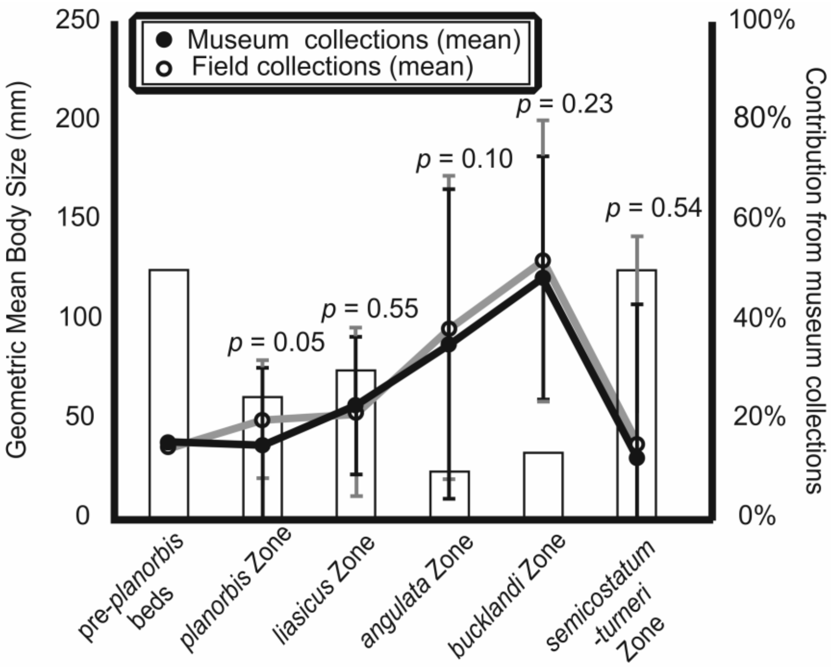

Figure 13. Variation in body size of Plagiostoma giganteum from museum collections (closed circles) and field observations (open circles). K-S test p values quoted for difference between museum collection and field sample. Error bars depict 95% confidence intervals. White bars show percentage of the time-binned sample that is comprised of museum specimens.

Location	Grid ref.	Section type	Basin	Formations	Zones studied	Depositional setting (Exc. Penarth Grp.)
1. Lavernock Point, Glamorgan	ST 188 682 – ST 183 679	Coastal	Bristol Channel	W – BL	Pre-planorbis – liasicus	Near basin margin becoming distal shelf
2. Nash Point, Glamorgan	SS 911 692 – SS 921 679	Coastal	Bristol Channel	BL	angulata – bucklandi	Distal shelf
3. Lilstock, Somerset	ST 178 453	Coastal	Bristol Channel	W – BL	Pre-planorbis – liasicus	Basinal, offshore, mud-dominated
4. East Quantoxhead, Somerset	ST 134 442 – ST 142 444	Coastal	Bristol Channel	BL	angulata – bucklandi	Basinal, offshore, mud-dominated
5. St. Audrie’s Bay, Somerset	ST 103 434 – ST 099 433	Coastal	Bristol Channel	W – BL	Pre-planorbis – liasicus	Basinal, offshore, mud-
6. Pinhay Bay, Devon	SY 317 907 – SY 333 914	Coastal	Wessex	L – BL	Pre-planorbis - bucklandi	Mud-dominated middle shelf
7. Charmouth, Dorset	SY 352 929 – SY 370 929	Coastal	Wessex	CM	semicostatum-turneri	Basinal, mud-dominated
8. Hock Cliff, Gloucestershire	SO 725 093	River cliff	Severn	BL	bucklandi	Mud-dominated middle shelf
9. Waterloo bay, Co. Antrim	NW 558 582	Coastal	Larne	W – WM	Pre-planorbis – planorbis,	Nearshore, silt-dominated
10. Portmuck Harbour, Co.	NW 558 582	Coastal	Larne	WM	planorbis	Nearshore, silt-dominated
11. Mochras, North Wales	SH 553 259	Drill core	Cardigan Bay		Pre-planorbis - turneri	Mud-dominated inner shelf
12. Redcar, North Yorkshire	NZ 613 253	Coastal	Cleveland	RM	angulata – bucklandi	Mud-dominated shelf
13. Robin Hood’s Bay, North Yorkshire	NZ 971 028	Coastal	Cleveland	RM	semicostatum-turneri	Silt-dominated shelf
14. Conesby Quarry, North Lincolnshire	SE 889 145	Quarry	East Midlands Shelf	SM	semicostatum	Wave-dominated shelf

Table 1. Details of field localities. Formation abbreviations: W = Westbury, BL = Blue Lias, L = Lilstock, CM = Charmouth Mudstone, WM = Waterloo Mudstone, RM = Redcar Mudstone, SM = Scunthorpe Mudstone.

Ammonite zone	**Plagiostoma giganteum**	**Antiquilima succincta**
semicostatum-turneri	173.60	52.45
bucklandi	179.97	162.34
angulata	152.75	145.67
liasicus	86.65	109.77
planorbis	74.20	74.83

Table 2. Comparison between maximum GMBS (mm), per ammonite zone, of Plagiostoma giganteum and Antiquilima succincta.

References

ABERHAN, M. 1994. Early Jurassic Bivalvia of northern Chile. Part 1. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia. *Beringeria*, **13**, 3–115.

———, SCHOLZ, A. and SCHUBERT, S. 2011. Das Ober-Pliensbachium (Domerium) der Herforder Liasmulde - Teil 3 - Taxonomie und Paläoökologie der Bivalvia aus der Amaltheenton-Formation (Unterjura) der Herforder Liasmulde. *Geologie und Paläeontologie in Westfalen*, **80**, 61–109.

ALROY, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science*, **280**, 731–734.

ARENDT, J. D. 2011. Size-fecuncity relationships, growth trajectories, and the temperature-size rule for ectotherms. *Evolution*, **65**, 43–51.

ATKINSON, D. 1994. Temperature and organism size—a biological law for ectotherms? *Advances in Ecological Research*, **25**, 1–58.

——— and SIBLY, R. M. 1997. Why are organisms usually bigger in cold environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*, **12**, 235–239.

ATTRILL, M. J., HARTNOLL, R. G., RICE, A. L. and THURSTON, M. H. 1990. A depth-related distribution of the red crab, Geryon trispinosus (Herbst) [=G. tridens KrÃ,yer]: indications of vertical migration. *Progress in Oceanography*, **24**, 197–206.

BARRAS, C. G. and TWITCHETT, R. J. 2007. Response of the marine infauna to Triassic – Jurassic environmental change : Ichnological data from southern England. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **244**, 223–241.

BELBEN, R. A., UNDERWOOD, C. J., JOHANSON, Z. and TWITCHETT, R. J. 2017. Ecological impact of the end-Cretaceous extinction on lamniform sharks. *PLoS ONE*, **12**, e0178294.

BERGMANN, C. 1847. Ueber die Verhältnisse der Wdrmeökonomie der Thiere zu ihrer Grösse. *Grottinger studien*, **3**, 595–708.

BERKE, S. K., JABLONSKI, D., KRUG, A. Z., ROY, K. and TOMASOVYCH, A. 2013. Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia world-wide. *Global Ecology and Biogeography*, **22**, 173–183.

BLOOS, G. and PAGE, K. N. 2002. Global stratotype section and point for base of the Sinemurian Stage (Lower Jurassic). *Episodes*, **25**, 22–28.

BONIS, N. R. 2010. Palaeoenvironmental changes and vegetation history during the Triassic-Jurassic transition.Unpublished PhD thesis, Utrecht University, Utrecht, 16-43pp.

———, RUHL, M. and KÜRSCHNER, W. M. 2010. Climate change driven black shale deposition during the end-Triassic in the western Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **290**, 151–159.

BOOMER, I. D., DUFFIN, C. J. and SWIFT, A. 1999. Arthropods 1: Crustaceans. *In* SWIFT, A. and MARTILL, D. M. (eds.) *Fossils of the Rhaetian Penarth Group*, The Palaeontological Association, London, 129–148 pp.

BORTHS, M. R. and AUSICH, W. I. 2011. Ordovician – Silurian Lilliput crinoids during the end-Ordovician biotic crisis. *Swiss Journal of Palaeontology*, **130**, 7–18.

BOTTINI, C., JADOUL, F., RIGO, M., ZAFFANI, M., ARTONI, C. and ERBA, E. 2016. Calcareous nannofossils at the Triassic/Jurassic boundary: Stratigraphic and paleoceanogrpahic characterization. *Rivista Italiana di Paleontologia E Stratigrafia*, **122**, 141–164.

BOTTRELL, S. and RAISWELL, R. 1989. Primary versus diagenetic origin of Blue Lias rhythms (Dorset, UK): evidence from sulphur geochemsity. *Terra Nova*, **1**, 451–456.

BROM, K. R., SALAMON, M. A., FERRÉ, B., BRACHANIEC, T. and SZOPA, K. 2015. The Lilliput effect in crinoids at the end of the Oceanic Anoxic Event 2 : a case study from Poland. *Journal of Paleontology*, **89**, 1076–1081.

BROWN, M. R., JEFFREY, S. W., VOLKMAN, J. K. and DUNSTAN, G. A. 1997. Nutritional properties of microalgae for mariculture. *Aquaculture*, **151**, 315–331.

CHEN, J., SONG, H., HE, W., TONG, J., WANG, F. and WU, S. 2018. Size variation of brachiopods from the Late Permian through the Middle Triassic in South China: Evidence for the Lilliput effect following the Permian-Triassic extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Published online 18 July 2018. doi:10.1016/j.palae.

CHEN, Y., TWITCHETT, R. J., JIANG, H., RICHOZ, S., LAI, X., YAN, C., SUN, Y., LIU, X. and WANG, L. 2013. Size variation of conodonts during the Smithian–Spathian (Early Triassic) global warming event. *Geology*, **41**, 823–826.

CHOWN, S. L. and GASTON, K. J. 2010. Body size variation in insects: a macroecological perspective. *Biological Reviews*, **85**, 139–169.

CHU, D., TONG, J., SONG, H., BENTON, M. J., SONG, H., YU, J. and QIU, X. 2015. Lilliput effect in freshwater ostracods during the Permian – Triassic extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **435**, 38–52.

CLÉMENCE, M.-E., BARTOLINI, A., GARDIN, S., PARIS, G., BEAUMONT, V. and PAGE, K. N. 2010. Early Hettangian benthic–planktonic coupling at Doniford (SW England): Palaeoenvironmental implications for the aftermath of the end-Triassic crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **295**, 102–115.

COPE, E. D. 1887. *The origin of the fittest* . D. Appleton and Co., New York.

COX, L. R. 1944. On Pseudolimea Arkell. *Proceedings of the Malacological Society, London*, **26**, 74–88.

———, NEWELL, N. ., BOYD, D. W., BRANSON, C. C., CASEY, R., CHAVAN, A., COOGAN, A. H., DECHASEAUX, C., FLEMING, C. A., HAAS, F., HERTLEIN, L. G., KAUFFMAN, E. G., MYRA KEEN, A., LAROCQUE, A., MCALESTER, A. L., MOORE, R. C., NUTTALL, C. P., PERKINS, B. F., PURI, H. S., SMITH, L. A., SOOT-RYEN, T., STENZEL, H.

B., TRUEMAN, E. R., TURNER, R. D. and WEIR, J. 1969. Part N bivalvia. *In* MOORE, R. C. (ed.) *Treatise on Invertebrate Paleontology*, The Geological Society of America, Inc. and The Universtiy of Kansas, N385–N393 pp.

CRAIG, G. Y. and HALLAM, A. 1963. Size-frequency and growth-ring analyses of Mytilus edulis and Cardium edule, and their palaeoecological significance. *Palaeontology*, **6**, 731–750.

DECONINCK, J., HESSELBO, S. P., DEBUISSER, N. and AVERBUCH, O. 2003. Environmental controls on clay mineralogy of an Early Jurassic mudrock (Blue Lias Formation , southern England). *International Journal of Earth Sciience (Geol Rundsch)*, **92**, 255–266.

DOMMERGUES, J.-L., MONTUIRE, S. and NEIGE, P. 2002. Size patterns through time: the case of the Early Jurassic ammonite radiation. *Paleobiology*, **28**, 423–434.

EPIFANIO, C. E. 1979. Growth in bivalve molluscs: nutritional effects of two or more species of algae in diets fed to the american oyster Crassostrea virginica (Gmelin) and the hard clam Mercenaria mercenaria (L.). *Aquaculture*, **18**, 1–12.

GALLOIS, R. W. 2007. The stratigraphy of the Penarth Group (late Triassic) of the east Devon coast. *Geoscience in South-West England*, **11**, 287–297.

———. 2008. The lithostratigraphy of the Shales-with-Beef Member of the Charmouth Mudstone Formation, Lower Jurassic. *Proceedings of the Ussher Scociety*, **12**, 32–40.

———. 2009. Lithostratigraphy of the Penarth Group (Late Triassic) of the Severn Estuary area. *Geoscience in South-West England*, **12**, 71–84.

GEIST, V. 1987. Bergmann’s rule is invalid. *Canadian Journal of Zoology*, **65**, 1035–1038.

HALLAM, A. 1960. A sedimentary and faunal study of the Blue Lias of Dorset and Glamorgan. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **243**, 1–44.

———. 1963. Observations on the palaeoecology and ammonite sequence of the Frodingham Ironstone (Lower Jurassic). *Palaeontology*, **6**, 554–574.

———. 1965. Environmental causes of stunting in living and fossil marine benthonic invertebrates. *Palaeontology*, **8**, 132–155.

———. 1975. Evolutionary size increase and longevity in Jurassic bivalves and ammonites. *Nature*, **258**, 493–496.

———. 1978. How rare is phyletic gradualism and what is its evolutionary significance? Evidence from Jurassic bivalves. *Paleobiology*, **4**, 16–25.

———. 1981. A revised sea-level curve for the early Jurassic. *Journal of the Geological Society*, **138**, 735–743.

———. 1987. Radiations and extinctions in relation to environmental change in the marine Lower Jurassic of Northwest Europe. *Paleobiology*, **13**, 152–168.

———. 1996. Recovery of the marine fauna in Europe after the end-Triassic and early Toarcian mass extinctions. *Geological Society, London, Special Publications*, **102**, 231–236.

———. 1998. Speciation patterns and trends in the fossil record. *GEOBIOS*, **30**, 921–930.

——— and EL SHAARAWY, Z. 1982. Salinity reduction of the end- Triassic sea from the Alpine region into northwestern Europe. *Lethaia*, **15**, 169–178.

HAMMER, Ø., HARPER, D. A. T. and RYAN, P. D. 2001. Past: Paleontological Statistics software package for education and data analysis. 9.

HARRIES, P. J. and KNORR, P. O. 2009. What does the 'Lilliput Effect' mean? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284**, 4–10.

HAUTMANN, M. 2004. Effect of end-Triassic CO2 maximum on carbonate sedimentation and marine mass extinction. *Facies*, **50**, 257–261.

HE, W.-H., TWITCHETT, R. J., ZHANG, Y., SHI, G. R., FENG, Q., YU, J. and WU, S. 2010. Controls on body size during the Late Permian mass extinction event. *Geobiology*, **8**, 391–402.

HESSELBO, S. P. and JENKYNS, H. C. 1995. Lower and Middle Jurassic of Dorset and Yorkshire. *In* TAYLOR, P. D. (ed.) *The Field Geology of the British Jurassic*, Geological Society of London, Bath, 110–115 pp.

HODGES, P. 1987. Lower Lias (Lower Jurassic) bivlavia from South Wales and adjacent areas.Unpublished PhD thesis, University College of Swansea, Swansea, 218-283pp.

HUANG, B., HARPER, D. A. T., ZHAN, R. and RONG, J. 2010. Can the Lilliput effect be detected in the brachiopod faunas of South China following the terminal Ordovician mass extinction? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **285**, 277–286.

JABLONSKI, D. 1996. Body size and macroevolution . *In* JABLONSKI, D., ERWIN, D. H. and LIPPS, J. H. (eds.) *Evolutionary Paleobiology*, University of Chicago Press, Chicago.

JAMES, A. C., AZEVEDO, R. B. R. and PARTRIDGE, L. 1995. Cellular basis and developmental timing in a size cline of Drosophila melanogaster. *Genetics*, **140**, 659–666.

JAMES, F. C. 1970. Geographic Size Variation in Birds and Its Relationship to Climate. *Ecology*, **51**, 365–390.

JARAULA, C. M. B., GRICE, K., TWITCHETT, R. J., BÖTTCHER, M. E., LEMETAYER, P., DASTIDAR, A. G. and OPAZO, L. F. 2013. Elevated p CO 2 leading to Late Triassic extinction , persistent photic zone euxinia , and rising sea levels. *Geology*, **41**, 955–958.

JOHNSON, A. 1994. Evolution of European Lower Jurassic Gryphaea (Gryphaea) and contemporaneous bivalves. *Historical Biology*, **7**, 167–186.

JOHNSON, M. E. and MCKERROW, W. S. 1995. The Sutton Stone: an Early Jurassic roky shore deposit in south Wales. *Palaeontology*, **38**, 529–541.

KAARIAINEN, J. I. and BETT, B. J. 2006. Evidence for benthic body size miniaturization in the deep sea. *Journal* *of the Marine Biological Association of the United Kingdom*, **86**, 1339–1345.

KALJO, D. 1996. Diachronous recovery patterns in Early Silurian corals, graptolites and acritarchs. *In* HART, M. B. (ed.) *Biotic Recovery from Mass Extinction Events*, Geological Society, London, Special Publications, vol. 102, 127–134 pp.

KAUFFMAN, E. G. and ERWIN, D. H. 1995. Surviving mass extinctions. *Geotimes*, **14**, 14–17.

KELLER, G. and ABRAMOVICH, S. 2009. Lilliput effect in late Maastrichtian planktic foraminifera : Response to environmental stress. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284**, 47–62.

KINGSOLVER, J. G. and HUEY, R. B. 2008. Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research*, **10**, 251–268.

KORTE, C., HESSELBO, S. P., JENKYNS, H. C., RICKABY, R. E. M. and SPOTL, C. 2009. Palaeoenvironmental significance of carbon- and oxygen-isotope stratigraphy of marine Triassic-Jurassic boundary sections in SW Britain. *Journal of the Geological Society*, **166**, 431–445.

KOSNIK, M. A., JABLONSKI, D., LOCKWOOD, R. and NOVACK-GOTTSHALL, P. M. 2006. Quantifying molluscan body size in evolutionary and ecological analyses: Maximizing the return on data-collection efforts. *Palaios*, **21**, 588–597.

LINSE, K., BARNES, D. K. A. and ENDERLEIN, P. 2006. Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 921–931.

LUTZ, R. A. 1976. Annual growth patterns in the inner shell layer of Mytilus edulis L. *Journal of the Marine Biological Association of the United Kingdom*, **56**, 723–731.

——— and RHOADS, D. C. 1980. Growth patterns within the molluscan shell. *In* RHOADS, D. C. and LUTZ, R. A. (eds.) *Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change*, Plenum Press, New York and London, 203–254 pp.

MANDER, L., TWITCHETT, R. J. and BENTON, M. J. 2008. Palaeoecology of the Late Triassic extinction event in the SW UK. *Journal of the Geological Society*, **165**, 319–332.

———, KÜRSCHNER, W. M. and MCELWAIN, J. C. 2013. Palynostratigraphy and vegetation history of the Triassic – Jurassic transition in East Greenland. *Journal of the Geological Society, London*, **170**, 37–46.

MARSHALL, L. G. and CORRUCCINI, R. S. 1978. Variability, evolutionary rates, and allometry in dwarfing lineages. *Paleobiology*, **4**, 101–119.

MARTÍNEZ-DÍAZ, L., PHILLIPS, G. E., NYBORG, T., ESPINOSA, B., DE ARAÚJO TAVORA, V., CENTENO-GARCÍA, E. and VEGA, F. J. 2016. Lilliput effect in a retroplumid crab (Crustacea: Decapoda) across the K/Pg boundary. *Journal of South American Earth Sciences*, **69**, 11–24.

MCELWAIN, J. C., BEERLING, D. J. and WOODWARD, F. I. 1999. Fossil plants and global warming at the Triassic-Jurassic boundary. *Science*, **285**, 1386–1391.

MCGOWAN, A. J., SMITH, A. B. and TAYLOR, P. D. 2009. Faunal diversity, heterogeneity and body size in the Early Triassic: Testing post-extinction paradigms in the Virgin Limestone of Utah, USA. *Australian Journal of Earth Sciences*, **56**, 859–872.

MCNAB, B. K. 1971. On the ecological significance of Bergmann's rule. *Ecology*, **52**, 845–854.

METCALFE, B., TWITCHETT, R. J. and PRICE-LLOYD, N. 2011. Changes in size and growth rate of 'Lilliput' animals in the earliest Triassic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **308**, 171–180.

MOGHADAM, H. V and PAUL, C. R. C. 2000. Trace fossils of the Jurassic, Blue Lias, Lyme Regis, southern England. *Ichnos*, **7**, 283–306.

MORTEN, S. D. and TWITCHETT, R. J. 2009. Fluctuations in the body size of marine invertebrates through the Pliensbachian-Toarcian extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284**, 29–38.

MORTON, J. D., WHITESIDE, D. I., HETHKE, M. and BENTON, M. J. 2017. Biostratigraphy and geometric morphometrics of conchostracans (Crustacea, Branchiopoda) from the Late Triassic fissure deposits of Cromhall Quarry, UK. *Palaeontology*, **60**, 349–374.

MOUSSEAU, T. A. 1997. Ectotherms follow the converse to Bergmann's rule. *Evolution*, **51**, 630–632.

NÜRNBERG, S., ABERHAN, M. and KRAUSE, R. A. 2012. Evolutionary and ecological patterns in body size, shape, and ornamentation in the Jurassic bivalve Chlamys (Chlamys) textoria (Schlotheim, 1820). *Fossil Record*, **15**, 27–39.

OLABARRIA, C. and THURSTON, M. H. 2003. Latitudinal and bathymetric trends in body size of the deep-sea gastropod Troschelia berniciensis (King). *Marine Biology*, **143**, 723–730.

PAGE, K. N. 2002. A review of the ammonite faunas and standard zonation of the Hettangian and Lower Sinemurian succession (Lower Jurassic) of the east Devon coast (south west England). *Geoscience in South-West England*, **10**, 293–303.

———. 2004. The East Midlands Shelf. *In* SIMMS, M. J., CHIDLAW, N., MORTON, N. and PAGE, K. N. (eds.) *British Lower Jurassic Stratigraphy, Geolocial Conservation Review Series No. 30*, Joint Nature Conservation Committee, Peterborough, 215–223 pp.

———. 2010. Stratigraphical Framework. *In* LORD, A. R. and DAVIS, P. G. (eds.) *Fossils from the Lower Lias of the Dorset Coast*, The Palaeontological Association, London, 33–53 pp.

PARIS, G., BEAUMONT, V., BARTOLINI, A., CLÉMENCE, M.-E., GARDIN, S. and PAGE, K. N. 2010. Nitrogen isotope record of a perturbed paleoecosystem in the aftermath of the end-Triassic crisis, Doniford section, SW England. *Geochem. Geophys. Geosyst*, **11**, 1–15.

PAYNE, J. L. 2005. Evolutionary dynamics of gastropod size across the end-Permian extinction and through the Triassic recovery interval. *Paleobiology*, **31**, 269–290.

PECK, L. S. and HARPER, E. M. 2010. Variation in size of living articulated brachiopods with latitude and depth. *Marine Biology*, **157**, 2205–2213.

POWELL, J. H. 2010. Jurassic sedimentation in the Cleveland Basin : a review. *Proceedings of the Yorkshire Geological Society*, **58**, 21–72.

PUGH, A. C., DANISE, S., BROWN, J. R. and TWITCHETT, R. J. 2014. Ecosystem dynamics following the Late Triassic mass extinction event : Palaeoecology of the Blue Lias Formation , Lyme Regis, UK. *Proceedings of the Ussher Scociety*, **13**, 255–266.

RADLEY, J. D., TWITCHETT, R. J., MANDER, L. and COPE, J. 2008. Disscussion on palaeoecology of the Late Triassic extinction event in the SW UK. *Journal of the Geological Society*, **165**, 988–992.

RENSCH, B. 1948. Histological changes correlated with evolutionary changes of body size. *Evolution*, **2**, 218–230.

RHOADS, D. C. and MORSE, J. W. 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia*, **4**, 413–428.

RICHARDSON, L. 1911. The Rhaetic and contiguous deposits of West, mid part of east Somerset. *Proceedings of the Geologists' Association, London*, **67**, 1–74.

RICHMOND, C., MARCUS, N. H., SEDLACEK, C., MILLER, G. A. and OPPERT, C. 2006. Hypoxia and seasonal temperature: Short-term effects and long-term implications for Acartia tonsa dana. *Journal of Experimental Marine Biology and Ecology*, **328**, 177–196.

RICHOZ, S., VAN DE SCHOOTBRUGGE, B., PROSS, J., PÜTTMANN, W., QUAN, T. M., LINDSTRÖM, S., HEUNISCH, C., FIEBIG, J., MAQUIL, R., SCHOUTEN, S., HAUZENBERGER, C. A. and WIGNALL, P. B. 2012. Hydrogen sulphide poisoning of shallow seas following the end-Triassic extinction. *Nature Geoscience*, **5**, 662–667.

ROY, K. and MARTIEN, K. K. 2001. Latitudinal distribution of body size in north-eastern Pacific marine bivalves. *Journal of Biogeography*, **28**, 485–493.

RUHL, M., DEENEN, M. H. L., ABELS, H. A., BONIS, N. R., KRIJGSMAN, W. and KÜRSCHNER, W. M. 2010. Astronomical constraints on the duration of the early Jurassic Hettangian stage and recovery rates following the end-Triassic mass extinction (St Audrie's Bay / East Quantoxhead, UK). *Earth and Planetary Science Letters*, **295**, 262–276.

SCHMIDT, D. N., THIERSTEIN, H. R. and BOLLMANN, J. 2004. The evolutionary history of size variation of planktic foraminiferal assemblages in the Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **212**, 159–180.

SHEPPARD, T. H. 2006. Sequence architecture of ancient rocky shorelines and their response to sea-level change: an Early Jurassic example from South Wales, UK. *Journal of the Geological Society, London*, **163**, 595–606.

———, HOUGHTON, R. D. and SWAN, A. R. H. 2006. Bedding and pseudo-bedding in the Early Jurassic of

Glamorgan: deposition and diagenesis of the Blue Lias in South Wales. *Proceedings of the Geologists' Association*, **117**, 249–264.

SHI, G. R., ZHANG, Y.-C., SHEN, S.-Z. and HE, W.-H. 2016. Nearshore-offshore-basin species diversity and body size variation patterns in Late Permian (Changhsingian) brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **448**, 96–107.

SHIRAYAMA, Y. 1983. Size structure of deep-sea meio- and macrobenthos in the western Pacific. *Internationale revue der gesamten hydrobiologie und hydrographie*, **68**, 799–810.

SIMMS, M. J. 2003. Uniquely extensive seismite from the latest Triassic of the United Kingdom : Evidence for bolide impact ? *Geology*, **31**, 557–560.

———. 2004*a*. The Mendip and South Wales massifs. *In* SIMMS, M. J., CHIDLAW, N., MORTON, N. and PAGE, K. N. (eds.) *British Lower Jurassic Stratigraphy*, Geological Conservation Review Series, No. 30, Joint Nature Conservation committee, Peterborough, 111–157 pp.

———. 2004*b*. The Severn Basin. *In* SIMMS, M. J., CHIDLAW, N. and MORTON, N. (eds.) *British Lower Jurassic Stratigraphy*, Geological Conservation Review Series, No. 30, Joint Nature Conservation committee, Peterborough, 164–170 pp.

——— and JERAM, A. 2007. Waterloo Bay, Larne, Northern Ireland: a candidate Global Stratotype Section and Point for the base of the Hettangian Stage and Jurassic System. *ISJS Newsletter*, **34**, 50–68.

SMITH, W. 1797. *An early list of strata by William Smith*. MSS pubulished by Douglas, J.A and Cox, L.R. (1949).

SOGOT, C. E., HARPER, E. M. and TAYLOR, P. D. 2014. The Lilliput effect in colonial organisms: Cheilostome bryozoans at the Cretaceous-Paleogene mass extinction. *PLoS ONE*, **9**, e87048.

SONG, H., TONG, J. and CHEN, Z. Q. 2011. Evolutionary dynamics of the Permian – Triassic foraminifer size : evidence for Lilliput effect in the end-Permian mass extinction and its aftermath. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **308**, 98–110.

SWIFT, A. 1999*a*. Stratigraphy (including biostratigraphy). *In* SWIFT, A. and MARTILL, D. M. (eds.) *Fossils of the Rhaetian Penarth Group*, The Palaeontological Association, London, 15–30 pp.

———. 1999*b*. Conodonts. *In* SWIFT, A. and MARTILL, D. M. (eds.) *Fossils of the Rhaetian Penarth Group*, The Palaeontological Association, London, 183–190 pp.

TWITCHETT, R. J. 2006. The palaeoclimatology , palaeoecology and palaeoenvironmental analysis of mass extinction events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 190–213.

———. 2007. The Lilliput effect in the aftermath of the end-Permian extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**, 132–144.

——— and BARRAS, C. G. 2004. Trace fossils in the aftermath of mass extinction events. *Geological Society, London, Special Publications*, **228**, 397–418.

URBANEK, A. 1993. Biotic crises in the history of Upper Silurian graptoloids: A Palaeobiological model. *Historical Biology*, **7**, 29–50.

VAN DE SCHOOTBRUGGE, B. and GOLLNER, S. 2013. Altered primary productivity during mass-extinction events. *The Paleontological Society Papers*, **19**, 87–114.

———, TREMOLADA, F., ROSENTHAL, Y., BAILEY, T. R., FEIST-BURKHARDT, S., BRINKHUIS, H., PROSS, J., KENT, D. V and FALKOWSKI, P. G. 2007. End-Triassic calcification crisis and blooms of organic-walled 'disaster species'. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **244**, 126–141.

VAN DER HAVE, T. M. and DE JONG, G. 1996. Adult size in ectotherms: Temperature effects in growth and differentiation. *Journal of Theoretical Biology*, **183**, 3329–340.

VAN VOORHIES, W. A. 1996. Bergmann size clines: A simple explanation for their occurrence in ectotherms. *Evolution*, **50**, 1259–1264.

VON ELERT, E., MARTIN-CREUZBURG, D. and LE COZ, J. R. 2003. Absence of sterols constrains carbon transfer between cyanobacteria and a freshwater herbivore (Daphnia galeata). *Proceedings of the Royal Society of London B*, **270**, 1209–1214.

WACKER, A. and VON ELERT, E. 2008. Body size and food thresholds for zero growth in Dressena polymorpha: a mechanism underlying intraspecific competition. *Freshwater Biology*, **53**, 2356–2363.

WARD, P. D., GARRISON, G. H., HAGGART, J. W., KRING, D. A. and BEATTIE, M. J. 2004. Isotopic evidence bearing on Late Triassic extinction events , Queen Charlotte Islands , British Columbia , and implications for the duration and cause of the Triassic / Jurassic mass extinction. *Earth and Planetary Science Letters*, **224**, 589–600.

WATERS, R. A. and LAWRENCE, D. J. D. 1987. *Geology of the South Wales Coalfield, part III, the country around Cardiff*. Memoirs of the Geological Survey, England and Wales. HMSO, London.

WEEDON, G. P. 1986. Hemi-pelagic shelf sedimentation and climatic cycles: The basal Jurassic (Blue Lias) of S. Britain. *Earth and Planetary Science Letters*, **76**, 321–335.

WEISS, M. B., CURRAN, P. B., PETERSON, B. J. and GOBLER, C. J. 2007. The influence of plankton composition and water quality on hard clam (Mercenaria mercenaria) populations across Long Island's south shore lagoon estuaries (New York, USA). *Journal of Experimental Marine Biology and Ecology*, **345**, 12–25.

WERONIKA, Ł., RODRÍGUEZ-TOVAR, F. J. and UCHMAN, A. 2017. Evaluating macrobenthic response to the Cretaceous-Palaeogene event : a high-resolution ichnological approach at the Agost section (SE Spain). *Cretaceous Research*, **70**, 96–110.

WIGNALL, P. B. 1990. Benthic palaeocology of the Late Jurassic Kimmeridge Clay of England. *Special papers in palaeontology*, **43**.

———. 2001. Sedimentology of the Triassic-Jurassic boundary beds in Pinhay Bay (Devon , SW England). *Proceedings of the Geologists' Association*, **112**, 349–360.

——— and HALLAM, A. 1991. Biofacies , stratigraphic distribution and depositional models of British onshore Jurassic black shales. *Geoogical Society Special Publications*, **58**, 291–309.

——— and BOND, D. 2008. The end-Triassic and Early Jurassic mass extinction records in the British Isles. *Proceedings of the Geologists' Association*, **119**, 73–84.

WOBBER, F. J. 1965. Sedimentology of the Lias (Lower Jurassic) of South Wales. *Journal of sedimentary petrology*, **35**, 683–703.