



Nearshore–offshore–basin species diversity and body size variation patterns in Late Permian (Changhsingian) brachiopods



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ABSTRACT

Body size is a fundamental and defining character of an organism, and its variation in space and time is generally considered to be a function of its biology and interactions with its living environment. A great deal of body size related ecological and evolutionary research has been undertaken, mostly in relation to extant animals. Among the many body size-related hypotheses proposed and tested, the *size–bathymetry* relationship is probably the least studied. In this study, we compiled a global body size dataset of Changhsingian (Late Permian, ca. 254 Ma–252 Ma) brachiopod species from low-latitude areas (30°S–30°N) and analyzed their species diversity and body size distribution patterns in relation to the nearshore–offshore–basin bathymetric gradient. The dataset contained 1768 brachiopod specimens in 435 species referred to 159 genera and 9 orders, from 135 occurrences (localities) of 18 different palaeogeographic regions. Treating the whole of the Changhsingian Stage as a single time slice, we divided the nearshore–offshore–basin bathymetric gradient into three broad depth-related environments: nearshore, offshore and basinal environments, and compared how the species diversity and body size varied along this large-scale bathymetric gradient.

Here, we report an array of complex patterns. First, we found a clear overall inverse correlation between species diversity and water depth along the nearshore–offshore–basin gradient, with most species concentrating in the nearshore environment. Second, when the median sizes of all low-latitude brachiopod species from the three environments were compared, we found that there was no significant size difference between the nearshore and offshore environments, suggesting that neither the wave base nor the hydrostatic pressure exerts a critical influence on the body size of brachiopods. On the other hand, the median sizes of brachiopods from the nearshore environment and, to a lesser extent, the offshore environment were found to be significantly larger than that of basinal brachiopods. This trend of significant size reduction in basinal brachiopods mirrors the relative low species diversity in the basinal environment, and neither can be easily explained by the tendency of decreasing food availability towards deeper sea environments. Rather, both trends are consistent with the hypothesis of an expanding Oxygen Minimum Zone (OMZ) in the bathyal (slope to deepsea) environments, where hypoxic to anoxic conditions are considered to have severely restricted the diversification of benthos and favored the relative proliferation of small-sized brachiopods. Finally, a significant difference was also found between eurybathic and stenobathic species in their body size response to the nearshore–offshore–basin gradient, in that eurybathic species (species found in all three environments) did not tend to change their body size significantly according to depth, whereas stenobathic forms (species restricted to a single environment) exhibit a decline in body size towards the basinal environment. This pattern is interpreted to suggest that bathymetrically more tolerant species are less sensitive to depth control with respect to their body size change dynamics, in contrast to stenobathic species which tend to grow larger in shallower water depths.

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1. Introduction

Body size is a fundamental and defining character of an organism, and its variation in space and time is generally considered to be intrinsic to its biology and also related to many aspects of its ecology (LaBarbera, 1989; Passy, 2012). As such, the quest to understand body size

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variations in space and time continues to be a central focus for biology, ecology and evolution (Blackburn and Gaston, 1998; Clausen and Erwin, 2008; Klug et al., 2015). A number of body size related ecological/evolutionary hypotheses have been proposed, notably including the following:

The size–temperature theory. There are two opposite aspects in this theory. One, widely known as the *Bergmann's rule*, predicts that body size of animals within the same clade tends to scale positively with increasing latitude or lower temperature (e.g., Chapelle and Peck, 1999; Hunt et al., 2010). By implication, this theory also predicts that global warming would result in overall size reduction for both individual organisms and communities (Daufresne et al., 2009; Sheridan and Bickford, 2011; Edeline et al., 2013). This relationship has indeed been found to apply to the Paleocene–Eocene Thermal Maximum event ~56 Ma (Secord et al., 2012; Yamaguchi et al., 2012) and to at least one Quaternary planktonic foraminiferan species (Malmgren and Kennett, 1978). The opposite idea (or the *size–energy theory*, see Hayward et al., 2009) suggests that body size on average decreases with increasing latitude due to reduced energy available per unit area at higher latitudes (e.g., Roy et al., 2000).

The *stunted growth theory* postulates that as global warming intensifies, marine $p\text{CO}_2$ increases and pH values decrease. Consequently, as a physiological response and adaptation strategy, marine organisms will become slower in growth and reproduction rate and hence increasingly dwarfed (Talmage and Gobler, 2011; Hönisch et al., 2012). Hallam (1963) provided some detailed discussions on this idea from both a theoretical background, as well as illustrations in its support based on the fossil record.

The *size–oxygen relationship* hypothesizes that the size of organisms scales positively with the amount of oxygen available in their habitats (Graham et al., 1995; Payne et al., 2013). A variant of this model, the *hyperoxia–gigantism hypothesis*, has been used to account for gigantism in some Late Palaeozoic terrestrial and marine species (Graham et al., 1995; Payne et al., 2012, 2013).

The *size–extinction risk theory* states that on average larger-bodied species live at lower densities than small-bodied ones (also known as the *size–abundance theory*, see Blackburn and Gaston, 1997; O'Gorman and Emmerson, 2011) and are hence subject to greater extinction risks over time (Jablonski, 1997). Despite being inconsistent with the *size–efficiency hypothesis* (Hülsmann et al., 2005), which predicts that on average larger bodied organisms are better competitors for resources and thus will outcompete smaller-sized species, the *size–extinction theory* has received strong empirical support from both living and fossil species (e.g., Lewis et al., 2008; Boyer and Jetz, 2010).

The *size–food relationship* predicts that the body size of many organisms scales positively with the resources (especially food) available in the environment. The existence of a body size hierarchy across trophic connections is widely accepted as a basic assumption of many food-web models (Shields and Hughes, 2009; Cheung et al., 2013).

The size–bathymetry hypothesis. This hypothesis may be seen as a direct application of the *size–food relationship* for aquatic species. It asserts that for most marine macrobenthic species their body size tends to scale negatively with water depth as a response to increasingly limited food availability in offshore environments (Thiel, 1975, 1979; Peck and Harper, 2010).

The *size–age relationship*, widely known as the *Cope's rule*, predicts that taxa in the same clade tend to increase size over time (Jablonski, 1997; Alroy, 1998; Novack-Gottshall and Lanier, 2008), although it remains unclear as to the drivers and mechanisms for this macroevolutionary trend over long timescales.

Among these hypotheses, the *size–bathymetry hypothesis* is probably the least studied. Ocean basin bathymetry is one of the most persistent and pronounced large-scale environmental gradients that have significant impact on the distribution of a wide range of biotic and ecological

variables impacting species diversity, abundance, replacement and turnover as well as body-size change dynamics (Jablonski et al., 1983; Sepkoski, 1991). Although some efforts have been made to reveal the relationship between the body size of marine faunas and the water depth associated with their habitats (e.g., Thiel, 1979; Rex and Etter, 1998; McClain et al., 2005), the conclusions reached thus far are inconsistent. For example, Thiel (1975, 1979) demonstrated that both the density and average body size of deep-sea benthos decrease with depth. While this conclusion has been confirmed in studies involving deep-sea gastropods (e.g., Olabarria and Thurston, 2003; Harasewych and Kantor, 2004) and Terebratulida brachiopods (Peck and Harper, 2010), a number of other studies have revealed opposite patterns, indicating, instead, a positive relationship between bathymetry and body size (Rex and Etter, 1998; Rex et al., 1999; McClain and Rex, 2001). Still a third pattern, though less common, has also been reported, pointing to either a lack of a persistent and stable correlation, negative or positive, between water depth and body size for at least some organisms (e.g., Polloni et al., 1979), or a highly complex non-linear relationship between body size and water depth (e.g., McClain et al., 2005).

Compared to the knowledge of the bathymetrical distributions of body sizes in extant marine taxa, that of the fossil record is significantly poorer due to much limited studies. Consequently, few of the above bathymetric patterns observed from living marine species have been tested with the fossil record. In this study, we aim to narrow this knowledge gap by undertaking a study of the body size distribution of Changhsingian (Late Permian, ca. 254–252 Ma) brachiopods in relation to ocean bathymetry. Specifically, we were interested in finding out whether the species diversity and median body sizes of Changhsingian brachiopods responded linearly, or nonlinearly, to the nearshore–offshore–basin bathymetric gradient of past ocean systems, and in understanding the mechanisms underpinning such patterns (or lack of them). To the best of our knowledge, this is the first such study undertaken on Permian brachiopods, although Peck and Harper (2010) have carried out a similar study of the size variation of living articulated brachiopods with latitude and water depth. A number of studies have been undertaken to test the nearshore–offshore gradient idea of brachiopod faunal change, replacement and evolutionary patterns using the fossil record (e.g., Ziegler, 1965; Fürsich and Hurst, 1974; Boucot, 1981; Patzkowsky, 1995; Pérez-Huerta and Sheldon, 2006; Tomašových, 2006; Clapham and Bottjer, 2007a,b; Bottjer et al., 2008; Chen et al., 2010, 2011; He et al., 2015), but none of these specifically investigated how body size of brachiopods varied along the nearshore–offshore–basin bathymetric gradient on a global scale.

Among fossil marine benthos, brachiopods are particularly suited to examine large-scale body size variations with water depth because of their distribution across an extreme wide range of water depths. Living brachiopods live at water depths ranging from a few meters to below 5000 m, although they are most diversified at species level in the offshore shelf environment (150–200 m) (Zezina, 2008, 2010). This broad bathymetric range is likely to be also true of fossil brachiopods although most of them, especially those from the Palaeozoic records, are known to have inhabited shallower water—mostly onshore—environments compared to their living counterparts (Harper and Moran, 1997).

Changhsingian (last stage of the Permian Period) brachiopods are of considerable global interest for body size studies because of their close association with the end-Permian mass extinction and with the widely recognized post-extinction Lilliput effect (Fraiser et al., 2005; Payne, 2005; He et al., 2007, 2010; Peng et al., 2007; Twitchett, 2007). Although Chen et al. (2010), Chen et al. (2011) and He et al. (2015) revealed some nearshore–offshore extinction patterns among Changhsingian brachiopods in South China, none specifically addressed the body size change patterns in relation to basin bathymetry. We therefore are still unsure of the role of bathymetry in enhancing or mitigating species extinction risks in relation to body sizes.

There is another added advantage in using Changhsingian brachiopods as the basis for the present study, that is the existence of a wealth of recent literature that not only has revised and modernized the taxonomy and biostratigraphy of Changhsingian brachiopod faunas globally (e.g., Chen et al., 2006; Shen and Shi, 2007; Posenato, 2011; Zhang et al., 2014; He et al., 2014), all these recent studies have also provided excellent illustrations of Changhsingian brachiopods, enabling the more accurate and more complete body size measurements of Changhsingian brachiopods.

2. Material and methods

2.1. Material

The term Changhsingian refers to the last stage of the Permian Period, spanning approximately 2.332–2.144 million years in duration (from 254.14 ± 0.07 to 251.902 ± 0.024 Ma), and is defined by a succession of six conodont biozones (*Clarkina wangi*, *Clarkina subcarinata*, *Clarkina changxingensis*, *Clarkina yini*, *Clarkina meishanensis*, *Hindeodus praeparvus*–*Hindeodus changxingensis* zones, in ascending order) (Shen et al., 2013). Using this definition in conjunction with other chronostratigraphical information, we compiled a global Changhsingian brachiopod dataset from 142 primary taxonomic references published up to the end of 2013 (see supplementary data files in Table S1 and Table S2). Because the vast majority (>80%) of the Changhsingian brachiopod records were from low latitude areas, we adopted a simple approach by focusing our analysis only on the palaeotropical (i.e., areas between 30°N and 30°S, primarily within the Palaeotethys) Changhsingian records, in a very similar approach taken by Zhang and Payne (2012). We standardized taxonomic assignments to species to the greatest extent possible prior to analysis, and removed any uncertain or indeterminate species. The final Changhsingian brachiopod database on which this study was based contained 135 occurrences (localities) from 18 different tectonic units, each of which represents a distinctive palaeogeographic entity during the Changhsingian. Among these 135 occurrences, there were 1768 brachiopod specimens, representing 435 species referred to 159 genera and 9 orders (Terebratulida, Spiriferinida, Spiriferida, Rhynchonellida, Productida, Orthotetida, Orthida, Lingulida and Athyridida) (Table 1).

The length and width of each brachiopod specimen was either compiled from the measurement information given in the original literature or measured from the published fossil images if no size data were provided. The suitability of using literature-based information for fossil body size studies has been investigated by Krause et al. (2007), who found that the size measurements of monographed specimens of

bivalves and brachiopods consistently record similar size classes for most species, hence suggesting that size data from published fossil images are useful for macroevolutionary studies of body size through time.

The volume of the brachiopods potentially could be used as a size proxy (Novack-Gottshall and Lanier, 2008), but is difficult to measure precisely due to their irregular geometric shape and often lack of shell thickness measurements in the literature, so it was not adopted in this study. In most previous studies, either length or width was used to represent brachiopod body size (e.g., Huang et al., 2010; Peck and Harper, 2010). However, because the Changhsingian brachiopods have many varied shapes with a considerable range in the length over width ratio (varying from 0.375 to 5.44), the selection of either length or width alone as a proxy of body size would potentially make the results biased. Consequently, we chose $\log_{10}(\text{length} \times \text{width})$ as the ultimate size metric for this study, similar to the approach taken by Berke et al. (2013) in their global study of the size–latitude relationships of marine Bivalvia. Importantly, we have found that this size metric is actually strongly correlated with either $\log_{10}\text{length}$ or $\log_{10}\text{width}$ (Fig. 1), and is complementary to the approach recommended for estimating the body size of molluscs (Kosnik et al., 2006).

For the purpose of this study, we classified Changhsingian brachiopod-bearing localities (depositional environments) into three broad depth-related environments, using the wave base and the shelf-slope break as critical discriminators: nearshore environments, offshore environments and deepsea or basinal environments (Fig. 2). The nearshore environment refers to benthic settings above the wave base, up to but usually less <50 m in water depth (Immenhauser, 2009), characterized by high oxygenation and strong hydrodynamic conditions. Common rock types of this environment are sandstone, siltstone and silty mudstone, locally mixed with some limestone. Some of the better known Permian–Triassic sections assigned to this environment include the Zhongzhai section (South China) and the Tesero section in the Dolomites (northern Italy). Offshore environments are located below the wave base but above the shelf break, and are typified by a relatively weak hydrodynamic condition, typically represented by mixed carbonate and siliciclastic rocks. It encompasses such settings in South China referred to by Chen et al. (2011) as shallow sea, reef buildups, platforms and shelf basins, also including seamounts and offshore carbonate platforms and their fringing slopes (ramps). Typical sections include the Meishan section (South China), the Balvany North section (Turkey), and the Akiyoshi Seamount Plateau (Japan). Basinal environments, the deepest of the three, are those situated in slope to bathyal settings, equivalent to the bathyal zone of Chen et al. (2011), usually associated with radiolarian (Albaillellaria)-bearing chert, shale, siliceous mudstone indicative of water depth ranging from 200 m to more than

Table 1
Summary of Changhsingian brachiopod species occurrences and measured specimens by region (tectonic block).

Region (tectonic block)	Palaeo-latitude	Number of occurrences	% of occurrences	Number of specimens	% of specimens
Akiyoshi terrane	24.275 N	1	0.74%	17	1%
Alps	3.191 N	9	6.67%	112	6%
Chanthaburi (Shan–Thai terrane, SE Asia)	19.372 S	2	1.48%	36	2%
Exotic Block (central Tibet)	23.906 S	1	0.74%	17	1%
Hungary	3.016 S	1	0.74%	13	1%
Indo-China	20.7 S	4	2.96%	9	1%
Italy	3.315 N	1	0.74%	2	0%
Lhasa block (southern Tibet)	24.302 S	1	0.74%	2	0%
Maizuru Belt (Japan)	22.914 N	1	0.74%	3	0%
North Caucasus	17.231 N	1	0.74%	10	1%
North Iran	4.913 N	7	5.19%	70	4%
Qamdo Block (central Western China)	16.865 S	3	2.22%	19	1%
South China	1.953 N	91	67.41%	1318	75%
Qaidam Block (northwest China)	19.783 N	2	1.48%	10	1%
South Kitakami (Japan)	27.237 N	1	0.74%	4	0%
South Pamir	12.775 S	7	5.19%	117	7%
Transcaucasia	4.169 S	1	0.74%	4	0%
Turkey	12.746 S	1	0.74%	4	0%
Total		135	100%	1767	100%

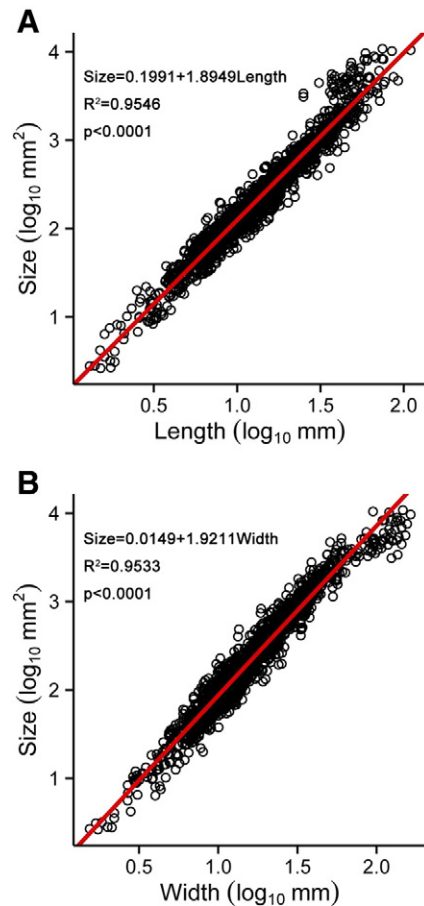


Fig. 1. Regression showing strong correlation of \log_{10} (length \times width) size with either body length or body width.

400 m (He et al., 2008). Changhsingian brachiopods of basinal environments referred to here are thus far only known from South China, typified by the Dongpan section, Majiashan section and the Shaiwa section (see details in online supplementary data Table S1).

We carried out statistical tests to see if the sampling regime used in constructing the Changhsingian brachiopod dataset was biased towards any particular environment or not. This was done by a bootstrap resampling analysis of species from the nearshore environment, which showed that the differences in maximum size between the nearshore environment and other environments were larger than could be explained simply by differences in diversity (bootstrap resampling test

using 10,000 replicates: nearshore versus offshore, $p < 0.0001$; nearshore versus basin, $p < 0.0001$). This means that size differences detected in this study between the three environments were not influenced (biased) by the number of species represented in each environment; in other words, the Changhsingian brachiopod dataset used for this study is sufficiently robust with respect to the purpose of the study. The high quality of the global palaeotropical Changhsingian brachiopod dataset, especially those from China which accounts for >70% in total occurrences and 77% in total specimens studied in this paper (Table 1), is also evident from a number of previous studies that have tested and verified the robustness in the sampling of Changhsingian brachiopod faunas through rarefaction analysis (e.g., Chen et al., 2011; He et al., 2015).

2.2. Statistical analysis

We used the largest specimen of each species in each environment. This approach has the potential to reduce the influence of juvenile or incomplete specimens and has been employed in previous body size studies (e.g., Rego et al., 2012; Zhang and Payne, 2012; Payne et al., 2013). We tested whether or not the size frequency distribution in each of the three environments followed the normal distribution using the Shapiro–Wilk test and found that none satisfied the test (nearshore: $W = 0.9784$, $p < 0.0001$; offshore: $W = 0.993$, $p = 0.0496$; basin: $W = 0.9845$, $p = 0.0208$) (Fig. 3). Consequently, we used the Mann–Whitney–Wilcoxon test, suited for non-parametric data, to compare and test for significant differences in the median sizes of the brachiopods among the three environments. In testing the intraspecific size differences between different environments, we also used the Mann–Whitney–Wilcoxon test to determine if the difference in median size between each pair of the environments was significant from zero. All statistical analyses were performed using R (version 3.0.3) (R Core Team, 2014).

3. Results

3.1. Nearshore–offshore–basin species diversity variation patterns

As shown in Fig. 2 and Table 2, the species diversity differs substantially among the three bathymetrically controlled environments, and the trend of their decline clearly follows the nearshore–offshore–basin bathymetric gradient. These differences are statistically significant (Mann–Whitney–Wilcoxon test, two-tailed $p = 0.1575$ for nearshore vs offshore comparison, $p = 0.01891$ for nearshore vs basin comparison, $p = 0.0268$ for offshore vs basin comparison) (Table 3) and cannot be explained by potential sampling bias because, as already outlined above, all the three environments are considered to have been

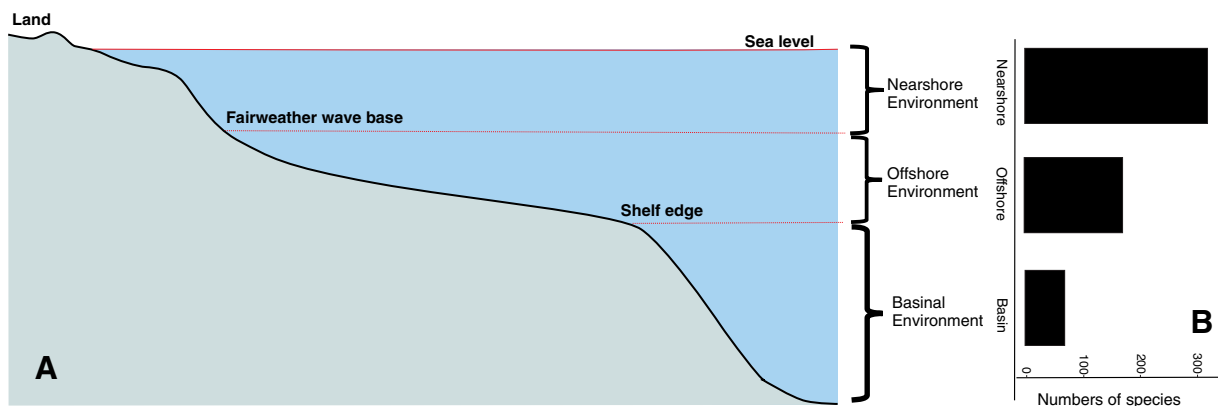


Fig. 2. Sketch showing the three broad benthic environments (nearshore, offshore and basin environments) along the nearshore–offshore–basin transect (A) and the distribution of palaeotropical (30°N–30°S) Changhsingian brachiopod species diversity within these three environments (B).

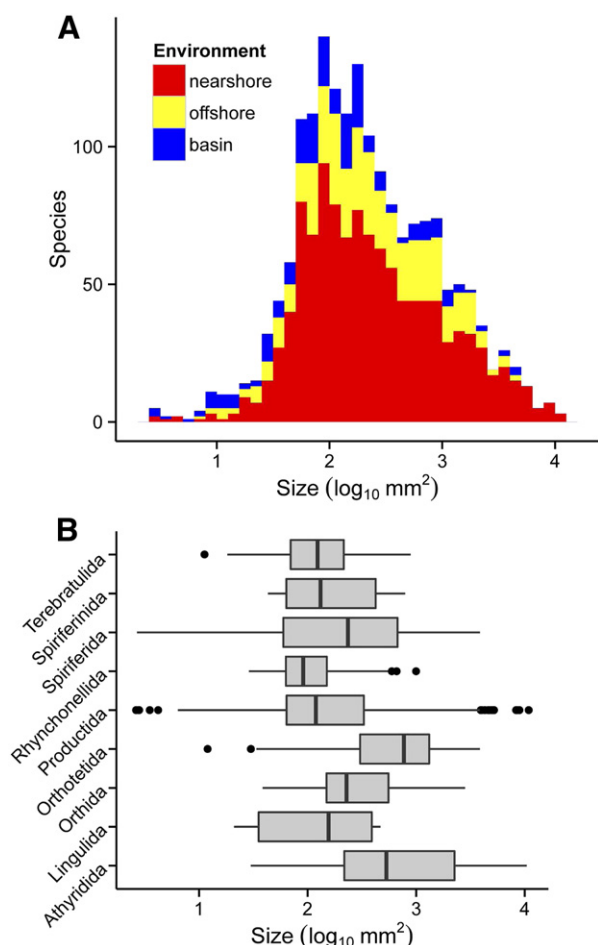


Fig. 3. Size distribution of all palaeotropical Changhsingian brachiopod species included in this study. (A) Size–frequency (species numbers) distribution by environment, showing non-normal distribution for any of the environment (also statistically proved so, see text for details). (B) Size range of brachiopod orders based on the size measurements of species within each order. Boxes represent interquartile range, with median indicated by the thick vertical black line. Whiskers indicate 5th and 95th percentiles while species beyond the 5th and 95th percentiles are indicated by black dots.

adequately sampled. With the exception of Terebratulida which is absent from the basinal environment, all other orders were found in all three environments. However, the species numbers of each order varied

Table 2
Distribution of brachiopod taxa by environment (upper table) and distribution of species within brachiopod orders by environment (lower table).

Number of taxa in each environment	Nearshore	Offshore	Basin	Subtotal
Number of specimens	1140	417	210	1767
Number of Species	320	170	67	557
Number of genera	127	95	40	262
Number of families	44	44	20	108
Number of Orders	9	9	8	26
<i>Distribution of species within orders in each environment</i>				
Terebratulida Waagen, 1883	23	16	0	39
Spiriferinida Ivanova, 1972	2	6	1	9
Spiriferida Waagen, 1883	42	22	5	69
Rhynchonellida Kuhn, 1949	29	16	3	48
Productida Sarytcheva and Sokolskaya, 1959	112	57	44	213
Orthotetida Waagen, 1884	46	27	9	82
Orthida Schuchert and Cooper, 1932	24	12	2	38
Lingulida Waagen, 1885	3	1	1	5
Athyridida Boucot, Johnson and Staton, 1964	39	13	2	54
Total	320	170	67	557

significantly between the environments. Among the nine orders, Productida were the most diversified across all environments, followed by Orthotetida, Spiriferida, Athyridida, Rhynchonellida, Orthida, Spiriferinida and Lingulida, with decreasing species diversity in that order (Table 2). Most of these orders, except Spiriferinida, also exhibit a within-clade decline in species numbers towards the basinal environment, mirroring the overall nearshore–offshore–basin species diversity decline trend in all species.

3.2. Nearshore–offshore–basin body size variation patterns

The Changhsingian brachiopods as a whole span more than four orders of magnitude in size variation, from 0.4195 to 4.0368 (Fig. 3A), and there are considerable differences in the range and variability of size variations among the different brachiopod orders (Fig. 3B). Overall, we found a significant difference in body size between nearshore and basinal environments (Mann–Whitney–Wilcoxon test, two-tailed $p = 0.0049$) (Fig. 4A, Table 3), but not so between nearshore and offshore environments (Mann–Whitney–Wilcoxon test, two-tailed $p = 0.1005$). There is also a visually obvious difference in median size between offshore and basinal environments although the difference was proved to be statistically insignificant (Mann–Whitney–Wilcoxon test, two-tailed $p = 0.1153$) (Fig. 4A). At first glance, the difference between nearshore and basinal environments seems to be accountable for by the difference in species richness between these two environments, but this suspicion was rejected by a bootstrap resampling test of species from the nearshore environment, which indicated that the difference in maximum size between the nearshore and the other two environments were larger than can be explained simply by differences in diversity (bootstrap resampling using 10,000 replicates: nearshore versus offshore, $p < 0.0001$; nearshore versus basin, $p < 0.0001$).

We also tested whether or not there were significant differences in body size within different clades across the three environments. We carried out this test first by comparing the median size distribution of brachiopod orders along the nearshore–offshore–basin gradient. With the exception of Spiriferida, no other orders show statistically significant differences in median sizes between environments. This result is unlikely to have been influenced by the uneven species numbers within the different orders as, for example, Productida has by far the largest species numbers in all three environments (Table 2), but yet the median sizes of its species across the three environments do not show significant differences. As for the Spiriferida, those from the basinal environment tend to have significantly smaller shells compared to those in nearshore and offshore environments (nearshore vs basin: Mann–Whitney–Wilcoxon test, two-tailed $p = 0.0129$; offshore vs basin: Mann–Whitney–Wilcoxon test, two-tailed $p = 0.0156$) (Table S3).

Next, we tested if there were significant body size differences within the species across different environments (i.e., intraspecific size difference). In our dataset, there were 22 eurybathic species that had been found occur in all three environments along the entire nearshore–offshore–basin gradient. A statistical test of the size distribution of these 22 species indicated no significant differences in the median size between the environments (nearshore vs offshore, Mann–Whitney–Wilcoxon test two tailed $p = 0.773$; offshore vs basin, Mann–Whitney–Wilcoxon test, two-tailed $p = 0.335$; nearshore vs basin, Mann–Whitney–Wilcoxon test, two-tailed $p = 0.6581$) (Fig. 5, Table 3). When these 25 species were grouped into their respective orders and were then reanalyzed at the order level for size difference, we found no tendency of intraspecific size changes between any pair of environments (Table S4).

Further, we also tested the size variation patterns of stenobathic species, namely species that were restricted (endemic) to a single bathymetric environment. We found that the median sizes of brachiopods endemic to either nearshore or offshore environment were significantly larger than the median sizes of species endemic to basinal environment (nearshore vs basin, Mann–Whitney–Wilcoxon test,

Table 3

Results of Wilcoxon two-sample test (t approximation) comparing median values of size distributions between environments for all brachiopod species and for species within individual orders. Bolded values indicate significant correlation. (Nns = number of nearshore species, Nos = number of offshore species, Nbs = number of basinal species).

	Types of statistical testing	Nearshore vs offshore	Nearshore vs basin	Offshore vs basin
Species diversity vs environment correlation test	Mann–Whitney–Wilcoxon test (comparing median values)	0.1575	0.01891	0.0268
Body size vs environment correlation test for all Changhsingian species	Mann–Whitney–Wilcoxon test (comparing median values)	0.1005	0.004874	0.1153
Body size vs environment correlation test for 25 eurybathic species that had been found in all three environments	Mann–Whitney–Wilcoxon test (comparing median values)	0.773	0.6581	0.335
Body size vs environment correlation test for stenobathic species that had been restricted to a single environment	Mann–Whitney–Wilcoxon test (comparing median values)	0.0583	0.0011	0.0271

two-tailed $p = 0.0011$; offshore vs basin, Mann–Whitney–Wilcoxon test, two-tailed $p = 0.0271$) (Fig. 6, Table S5). However, there was no tendency for significant size differentiation in the largest specimens of the endemic species between nearshore and offshore environments (Mann–Whitney–Wilcoxon test, two-tailed $p = 0.0583$). Once the endemic species were placed in their respective orders, which were

then compared and tested for size differences, we found no significant differences between orders in the nearshore–offshore–basin size comparisons, with the only exception of Spiriferida whose endemic species tend to demonstrate a significant decline in median sizes along the nearshore–offshore–basin gradient (nearshore vs basin: Mann–Whitney–Wilcoxon test, two-tailed $p = 0.0197$; offshore vs

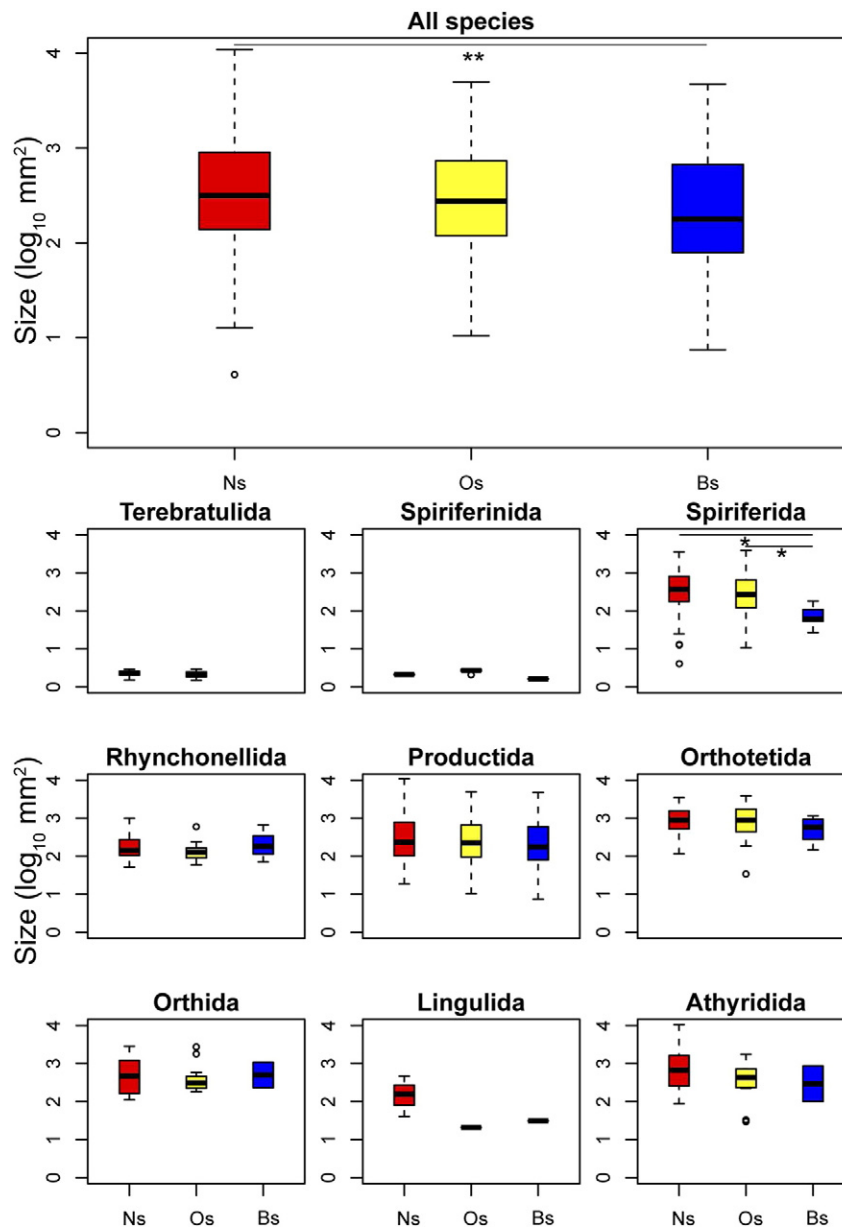


Fig. 4. Comparison of size distributions of species among the nearshore, offshore and basin environments. Top figure includes all species, bottom figures refer to species within each order. Boxes and whiskers as in Fig. 3. * $p < 0.05$; ** $p < 0.01$. Significance levels of all comparisons are presented in Table S3.

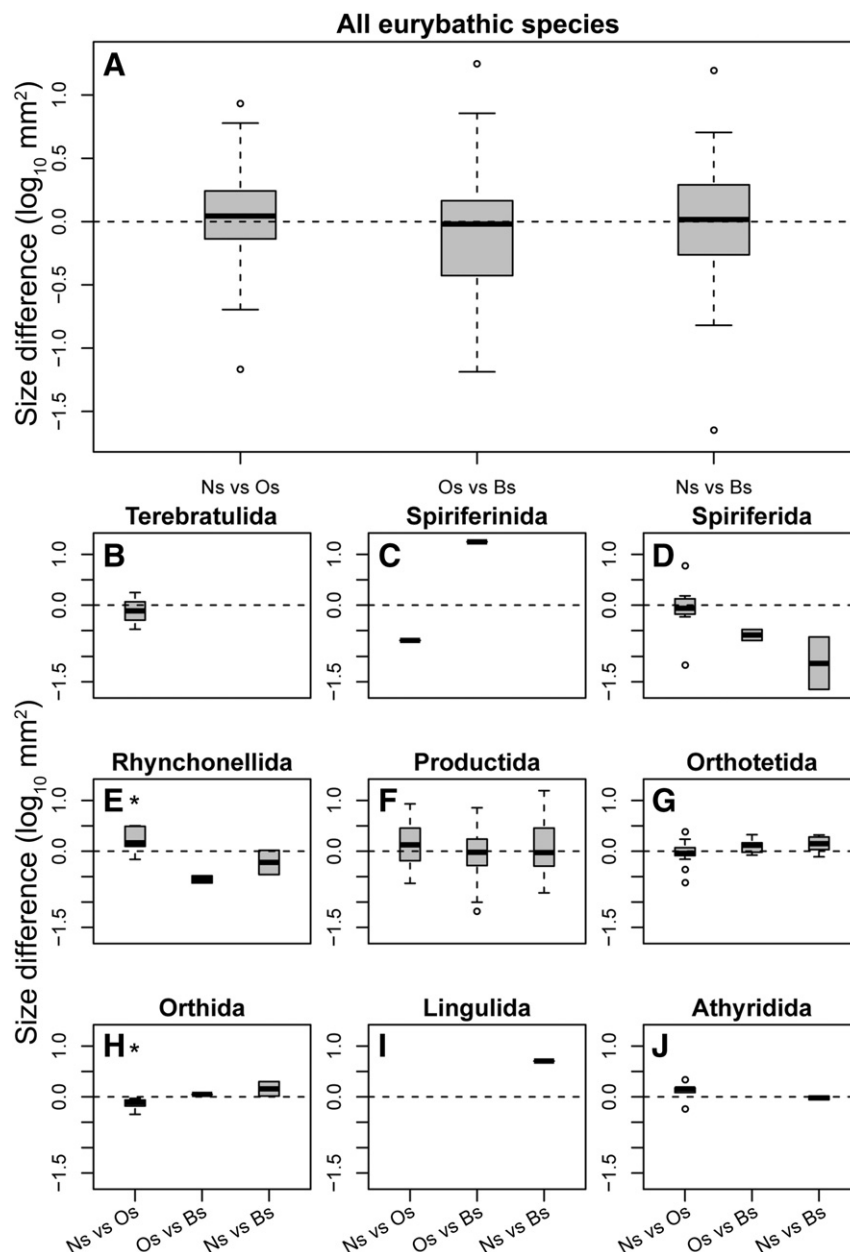


Fig. 5. Comparison of size distributions of eurybathic species among the nearshore, offshore and basin environments (i.e., intraspecific size comparisons between environments). Top figure includes all eurybathic species ($N = 22$), bottom figures refer to eurybathic species within each order. Boxes and whiskers as in Fig. 3. * $p < 0.05$. Significance levels of all comparisons are presented in Table S2.

basin: Mann–Whitney–Wilcoxon test, two-tailed $p = 0.0172$) (Table S5).

4. Discussion

Summarizing the above analyses and outcomes, we can note two very interesting findings. First, there is a clear and strong overall inverse correlation between species diversity and water depth, as is between brachiopod median size and water depth, along the nearshore–offshore–basin gradient (Fig. 2). Second, among those eurybathic species that existed across the entire nearshore–offshore–basin gradient, there were no significant size differences found between the environments (Fig. 5), while significant size differences were observed for stenobathic species between nearshore and basinal environments or between offshore and basinal environments (Fig. 6).

4.1. Controls on species diversity and body size changes along the nearshore–offshore–basin gradient

With regard to the pronounced species diversity and body size decline with water depth, similar patterns have long been noted in many groups of both extant and fossil brachiopods (e.g., Fürsich and Hurst, 1974; Zvezina, 2008; Peck and Harper, 2010), but the explanation to account for these coupled nearshore–offshore–basin gradient patterns (i.e., similar patterns in species diversity and body size changes along the same gradient) is not straightforward and cannot be simply attributed to water depth alone.

A multiplicity of factors, including oxygen and food availability, have been proposed to explain varied patterns of species diversity and body size variations along the nearshore–offshore–basin gradient (e.g., Fürsich and Hurst, 1974; Pérez-Huerta and Sheldon, 2006; He et al., 2007; McCallum et al., 2015). In most of these studies, the

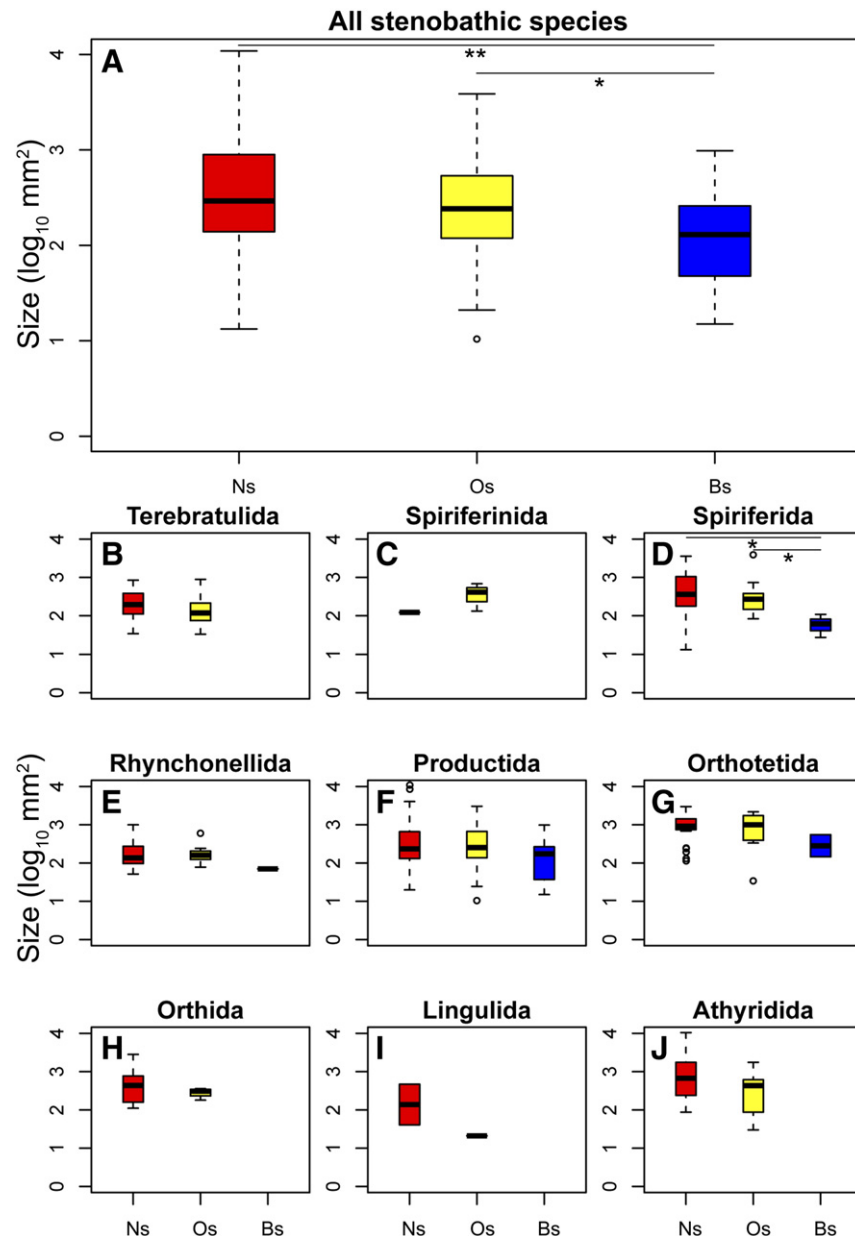


Fig. 6. Comparison of size distributions of stenobathic species among the nearshore, offshore and basin environments (i.e., inter-specific size comparisons between environments). Top figure includes all stenobathic species, bottom figures refer to stenobathic species within each order. Boxes and whiskers as in Fig. 2. * $p < 0.05$; ** $p < 0.01$. Significance levels of all comparisons are presented in Table S3.

emphasis has been placed on the crucial importance of food relative to oxygen, but there is no consensus as to which of the two plays a more primary role in affecting the spatial distribution of brachiopod species diversity and body size in a nearshore–offshore–basin transect situation. Generally speaking, food availability and oxygen concentration are the two most important determinants of animal body sizes, and, interestingly, neither changes linearly with water depth in global ocean systems due to the presence of the thermocline, the Oxygen Minimum Zone (OMZ) and/or coastal upwelling systems (Levin, 2003; Zvezina, 1997, 2000). According to Levin (2003), OMZs typically occur in bathyal depths and are typically characterized by oxygen depletion (hypoxic to anoxic conditions) but with relative high primary productivity (food availability). Marine benthos preadapted to living in these environments are usually of low diversity, high abundance, small body size and thin shelled. In our study, the basal environment largely overlaps with the OMZ as defined by Levin (2003). It is therefore

tempting to suggest that the overall smaller body size (and also relatively lower species diversity) of Changhsingian brachiopods that lived in this environment could be considered as a natural response (adaptation) to low oxygen conditions. This is so because small-bodied organisms have an advantage in maximizing oxygen intake by presenting a larger surface area/volume ratio in the absence of sufficient oxygen (Levin, 2003; Peng et al., 2007).

Accepting this scenario, the role of primary productivity and food availability in influencing brachiopod body size dynamics must, therefore, be considered secondary at most, not the least for those adapted to living in OMZs. This observation is strongly consistent with two recent studies investigating the spatial and temporal distribution of Changhsingian phytoplankton in South China (Lei et al., 2012; Shen et al., 2014). According to Lei et al. (2012), both the genus and species diversity of Changhsingian phytoplankton in South China demonstrate a strong nonlinear trend with the nearshore–offshore bathymetric

gradient with the highest diversity occurring in the ‘offshore’ environment ranging from the outer shelf to upper slope (hence encompassing the offshore and the upper part of the basinal environment referred to in this study). Yet, both the species diversity and median brachiopod body size of these environments are significantly small relative to the nearshore settings, suggesting insignificant impact of primary productivity on brachiopod body size variations. Although there appears to be a strong, albeit nonlinear, spatial variation in Changhsingian primary productivity across South China, phytoplankton production appears quite stable stratigraphically throughout the Changhsingian, at least for the basinal environment. According to Shen et al. (2014), who, based on two deep-water sections in South China (Xiakou and Xinmin sections), found that primary productivity remained relatively high in basinal environments in the Changhsingian until the very end of this interval (equivalent to *C. meishanensis* Zone) when the primary production in the photic zone crashed and primary producers changed abruptly from calcareous algae to stress-tolerant acritarch and cyanobacteria, thereafter it remained low from the latest Changhsingian *C. meishanensis* Zone through to the *H. parvus*–*I. isarcica* Zone of the earliest Triassic. The initiation and maintenance of relatively high primary productivity in South China through most parts of the Changhsingian to the earliest Triassic has been attributed to enhanced upwellings and an expanding OMZ, as evident from both empirical evidence (e.g., Song et al., 2012) and also from model simulations (Olsen et al., 2013).

Based on a study of brachiopod body size stratigraphic variations in concert with a range of environmental factors (sea level change, lithology, terrestrial flux, primary productivity using radiolarians as zooplankton indicators) at the Dongpan section (basin environment), He et al. (2007) drew a possible link between late Changhsingian brachiopod miniaturization and lowered pelagic primary productivity (following the extinction of radiolarians) while also noting an increase of potential terrestrial food resources to the basinal environment due to increased terrestrial fluxes in the late Changhsingian. Thus, we seem to face a paradoxical situation here with respect to the possible effects of the interplay between reduced pelagic primary productivity (due to the extinction of radiolarians) and increased terrestrial food resources (due to increased terrestrial fluxes) on brachiopod body size changes. Not discounting nutrient as a potentially crucial determinant influencing brachiopod body size, He et al. (2007) explained the apparent paradox by suggesting that increased turbidity and low-quality food, induced by the increased terrestrial fluxes, coupled by the decreased pelagic food resources (due to the extinction of radiolarians), would have caused stunted growth among the basinal brachiopods by retarding their feeding mechanisms. In a later follow-up study based on another basinal Permian–Triassic section (Majiashan section) in South China, He et al. (2010) did not find any coherent and stratigraphically consistent correlation between oxygen (measured by Ce, a rare earth element) and size change patterns, nor between body size change trends and primary productivity (as measured by Ni and Cu trace elements) and abundance of acritarchs, therefore rejecting primary productivity or oxygen as the main or the only controlling factor on brachiopod size change. Instead, they inferred that brachiopod size increase was due to loss of competitors allowing the remaining, most extinction-resistant species to gain relatively larger size even when the food resources or oxygen contents were limited.

4.2. How important was the wave base and substrate condition in influencing brachiopod body size changes along the nearshore–offshore–basin gradient?

In addition to oxygen and food, hydrodynamic conditions, usually expressed as a degree of water movement in the environment, potentially could also have exerted significant influence on the body size change dynamics of brachiopods (Alexander, 1984). In our study, this probability was tested by investigating whether or not the wave base

and the shelf break constituted boundaries of major discontinuities in the Changhsingian brachiopod body size spectra along the nearshore–offshore–basin gradient. As shown in Figs. 2 and 3, there was no overall size differences between nearshore and offshore environments, either in terms of species found common to both environments or in terms of species endemic to a single environment. This suggests that the wave base was not an effective barrier in differentiating size groups of brachiopod species. This finding is consistent with Groves et al. (2012) who found that the distribution of upper Pennsylvanian fusuline test sizes was unrelated to substrate hydrodynamic conditions. Although it was beyond the scope of this study to specifically explore the potential relationship between Changhsingian brachiopod body size and substrate type, He et al. (2015)’s recent study did shed some light on this aspect. These authors compared the timing of Changhsingian brachiopod size changes across multiple water depths and varied substrate facies and found no evidence demonstrating significant influence of substrate types on body size change dynamics. Instead, they found that either body size changed regardless of lithology (e.g., body size change still occurred even in the absence of lithological change), or that lithology evidently changed but involving no significant body size change.

On the other hand, brachiopods endemic to nearshore and offshore environments were found significantly larger than the brachiopods endemic to the basinal environment (Fig. 6, Table S5). This is a difficult pattern to explain by any single physical factor, but the shelf break, taken here to mark the boundary between offshore and basinal environments (Fig. 1), is likely to have played a crucial role in causing this distinct discontinuity in the nearshore–offshore–basin spectra of brachiopod size distributions. In proposing this scenario, instead of suggesting water depth itself as the driver for the size break, we argue that lowered oxygen, as would be expected if South China, during the Changhsingian, was under the influence of a rapidly expanding OMZ and enhanced upwelling regimes, as suggested above, would be the most direct (proximate) agent causing both stunted growth and poorer species diversity of brachiopods in basinal environments.

4.3. Taxonomic and ecological dependence of body size change patterns along the nearshore–offshore–basin gradient

This study compared the body size change patterns along the nearshore–offshore–basin gradient at two taxonomic levels: species and orders. For most comparisons, the patterns recognized are consistent regardless of the taxa used, pointing to the robustness of the patterns detected. In a few cases, however, there appear to be some interesting taxonomic variations. The test comparing the median size distribution of brachiopod orders along the nearshore–offshore–basin gradient showed that among the nine brachiopod orders studied, only Spiriferida demonstrated a significant difference between the basin and the other environments in that those from basinal settings tend to have significantly smaller shells compared to those in nearshore and offshore environments (Table S3). Although this finding is consistent with what Fürsich and Hurst (1974) had already observed with regard to Silurian (Wenlock) spiriferids, it should be noted that only five species of Spiriferida in our dataset were shown to be present in the basin environment compared to 42 and 22 spiriferid species present respectively in nearshore and offshore environments (Table 2). Of these five species, two also occur in the latter environments, and the remaining three species are restricted to the basinal environment and they are the ones that demonstrate significantly smaller sizes than the spiriferid species in nearshore and offshore environments.

At the species level, the body size response to the nearshore–offshore–basin depth gradient revealed some interesting differences between eurybathic and stenobathic species: eurybathic species do not tend to change their body size significantly according to depth, whereas the median sizes of stenobathic brachiopods endemic to either nearshore or offshore environment were significantly larger than the

median sizes of species endemic to the basinal environment. This revelation is interesting and suggests that bathymetrically more tolerant (or wide-ranging) species are also less sensitive to depth control with respect to their body size change dynamics, in contrast to stenobathic species which tend to grow larger in shallower water depths.

The finding that stenobathic Spiriferida species in nearshore and offshore environments tended to be significantly larger than those in the basinal environment whereas Productida failed to demonstrate such differences (Fig. 6, Table S5) is in good agreement with Pérez-Huerta and Sheldon (2006) who also revealed that larger Pennsylvanian spiriferid-dominated brachiopod communities tended to prevail more in shallower water environments due to not only their larger and robust shells in enduring high-energy conditions but also their much enhanced filter-feeding ability in capturing and digesting food in such high-nutrient settings. These authors also found that, in contrast to spiriferids, productids, on the other hand, are much less common in shallower waters but dominated in deeper environments as they were able to compensate for the much reduced food supply in such settings by the development of multi-directional inhalant currents (thus maximizing food intake in a given time).

4.4. Changhsingian brachiopod body size change dynamics and the end-Permian mass extinction

Notwithstanding some taxonomic and ecological (eurybathic vs stenobathic) variations in demonstrating body size change patterns along the nearshore–offshore–basin gradient, as noted above, that the median size of basinal Changhsingian brachiopod species as a whole was significantly smaller than those of the nearshore and basinal environments is a significant revelation and requires discussion. Was it an expression of preadaptation to living in an Oxygen Minimum Zone (OMZ) or a situational (i.e., un-precipitated or unprepared) response to a global but transient environmental disturbance? The first scenario assumes permanent dwarfism of marine benthos in OMZs compared to other marine environments, whereas the latter scenario does not make such an assumption and, instead, assumes that community dwarfism is a temporal response to a sudden unexpected environmental perturbation such as hypoxia, hyperthermia, hypercapnia, or ocean acidification, each or a combination of which temporarily is able to suppress animal growth across the community. Elsewhere we have already suggested the possibility of hypoxia, invariably associated with OMZ, as the most likely stressor for causing body size reduction among Changhsingian basinal brachiopods, but this interpretation does not and should not exclude the second scenario. Unfortunately, the temporal resolution employed in the present study does not permit us to test the validity of one scenario against another, but a recent idea proposed by He et al. (2015) is worth noting here. While revealing a notably earlier occurrence of basinal Changhsingian brachiopod extinctions in South China compared to their counterparts in shallow water settings, He et al. (2015) also noted significant brachiopod body size reduction immediately preceding their extinctions. These authors attributed both the body size reduction and the earlier occurrence of deepwater extinctions to the initiation and rapid expansion of the OMZ and its associated chemocline in the bathyal environment in response to an abrupt global warming event, by considering these biotic changes as direct responses to an increasingly anoxic, nutrient-depleted bathyal environment and by the presence of lithological feature and trace fossil which indicates oxygen restriction. If He et al. (2015) is followed, the dwarfism of Changhsingian brachiopods in the basinal environment compared to brachiopod body size spectra in other environments could also be interpreted as a temporal response to the rise and intensification of hypoxia to anoxia conditions in the basinal environments, probably driven by a rapidly expanding and upward migrating OMZ.

5. Conclusions

This study has revealed an inverse correlation between species diversity, median body size and water depth of palaeotropical Changhsingian brachiopods along the nearshore–offshore–basin bathymetric gradient. Overall, there were more and larger-sized Changhsingian brachiopod species in the nearshore and offshore environments than they were in deeper water basinal settings, and there was no significant size difference between the nearshore and offshore environments. These apparently linear nearshore–offshore–basin patterns cannot be explained by the presence or absence of the wave base, nor can they be simply correlated with and attributed to water depth or decline of primary productivity. Instead, an active Oxygen Minimum Zone (OMZ) is invoked here to account for the observed nearshore–offshore–basin species diversity and body size change trends. A rapidly expanding OMZ would have caused widespread hypoxic to anoxic conditions in palaeotropical oceans during the Changhsingian, which in turn would have severely restricted the diversification of large benthos in bathyal habitats but favored the relative proliferation of small-sized brachiopods in these settings. The study also found significant difference between eurybathic and stenobathic species in their body size response to the nearshore–offshore–basin gradient, in that eurybathic species did not tend to change their body size significantly according to depth, whereas stenobathic forms exhibit a decline in body size towards the basinal environment. This pattern is interpreted to indicate that bathymetrically more tolerant (or wide-ranging) species are less sensitive to depth control with respect to their body size change dynamics, in contrast to stenobathic species which tend to grow larger in shallower water depths.

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