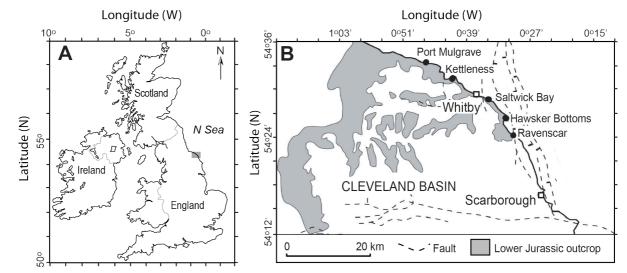
- **1** Supporting online material for 'Primary productivity controls
- 2 on opportunistic bivalves during Early Jurassic oceanic
- 3 deoxygenation'
- 4 Bryony A. Caswell and Angela L. Coe

## 5 1. Methods

# 6 Supplementary information on field data collection

- 7 Shell size and abundance data for the epifaunal bivalves
- 8 Pseudomytiloides dubius and Bositra radiata (Fig. DR2) were collected from
- 9 the shallowly dipping and laterally extensive foreshore exposures along the
- 10 north Yorkshire coast, UK at Port Mulgrave (54°32'48.64"N 00°45'59.50"W),
- 11 Kettleness (54°31'50.56"N 00°43'12.25"W), Saltwick Bay (54°31'15.84"N
- 12 00°35'15.68"W), Hawsker Bottoms (54°27'29.89"N 00°33'25.62"W) and
- 13 Ravenscar (54°24'23.37"N 00°29'19.03"W) and (Fig. DR1). Data were
- 14 collected during seven weeks of fieldwork spanning a two year period. Almost
- 15 all fieldwork was undertaken in late autumn to early spring after stormy
- 16 conditions and/ or spring tides in order to maximize the amount and freshness
- 17 of the foreshore exposures.



18 19

20 Figure DR1. Field study area. A: Map of the UK. Grey box shows area covered by B. B: Map

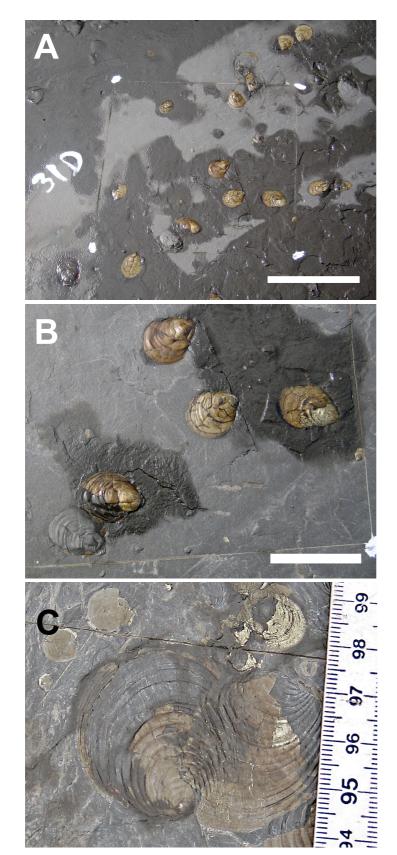
 $21\,$   $\,$  of the Cleveland Basin showing the Lower Jurassic outcrop, fault lines, and the five field study  $\,$ 

- 22 sites on the Yorkshire coast: Hawsker Bottoms, Port Mulgrave, Kettleness, Saltwick Bay,
- 23 Hawsker Bottoms and Ravenscar (figure modified from Rawson and Wright (1995)).

24	The stratigraphic positions of the sampled bedding planes were
25	recorded at 0.5 cm resolution with respect to known stratigraphic datums (e.g.
26	bed boundaries of Howarth, 1992) based on the graphic log of Kemp <i>et al.</i>
27	(2005) and Kemp (2006). Care was taken to ensure data were from one
28	stratigraphic level by removing overlying clay laminae and fossils to expose a
29	single lamina. Each stratigraphic level was interpreted to represent one
30	temporal point and thus one time averaged population. Quadrats (20 cm x 20
31	cm) were marked out and multiple high-resolution images were taken (e.g.
32	Fig. DR2A). From these photographs bivalve abundance was determined and
33	shell size (length and surface area) measured using image analysis (ImageJ
34	1.41i, National Institute of Health). At stratigraphic levels where the density of
35	P. dubius was 24 individuals or less the abundance was recorded but the
36	shells were not measured.
37	Data were collected at the highest resolution that their stratigraphic
38	occurrences would allow over the main interval of the event (-3.71 m to 5.8
39	m), and at a roughly decimetre scale stratigraphic resolution above and below
40	this. The resulting average stratigraphic resolution is summarized in Table
41	DR1, and true heights are provided in Figure DR2. It is noteworthy that
42	previous biotic studies through the OAE are at a 10–50 fold (Little, 1996)
43	lower stratigraphic resolution and at any one stratigraphic level have a mean
44	sample size 13-24 fold lower (Morten and Twitchett, 2009) than this study.
45	

Ammonite zone(s)	Ammonite subzones	Height (m)	Mean (range) strat. resolution (cm)
Bivalve abundance data			
Dactylioceras (Orthodactylites) tenuicostatum (Young & Bird)	Protogrammoceras (Paltarpites) paltum Buckman to D. (O.) semicelatum (Simpson)	-14 to 0	11.0 (0.1–91)
Harpoceras falciferum (J. Sowerby)	<i>H. falciferum</i> and <i>Cleviceras exaratum</i> (Young & Bird)	0 to 16	4.5 (0.1–73)
H. falciferum to Hildoceras bifrons Bruguiere	H. falciferum and D. commune (J. Sowerby)	16 to 35	11.0 (0.2–508)
Bivalve size data			
D. tenuicostatum to H. falciferum	D. (O.) semicelatum to H. falciferum	-3.71 to 21.37	11.0 (0.2–87)
Note: zero datum is the base of b	ed 33 of Howarth (1992; Fig. DR3)		

TABLE DR1: RESOLUTION OF THE FIELD COLLECTED DATA



47



Figure DR2. The two dominant bivalve species found in the strata representing the Toarcian
OAE near Whitby, Yorkshire, UK. A: *Pseudomytiloides dubius* specimens in a 20 cm x 20 cm
quadrat from 2.05 m below the middle of bed 35 (the Whalestone Nodules) at Port Mulgrave;
scale bar is 10 cm. B: Close up of A; scale bar is 4 cm. C: *Bositra radiata* from 132 cm below

- 54 the middle of bed 33 (the Canon Ball Nodules) at Port Mulgrave; scale in centimetres.
- 55

### 56 Supplementary information on data analyses

57 All statistical analyses (linear and multiple regressions, and non-

58 parametric tests) were performed on SPSS v. 20 (http://www-

59 01.ibm.com/support/docview.wss?uid = swg24029274) except for reduced

60 major axis regressions that were performed with Past.exe (Hammer et al.,

61 **2001**).

### 62 Multiple regression

Results from multiple regression were analysed for multicollinearity
(variance inflation factors), autocorrelation (Durbin-Watson), and the influence
of extreme cases (leverage values, Cooks distance, Mahalanobis distances,
DFBeta statistics, and covariance ratios). Residuals were inspected for
heteroscedasticity, non-linearity and non-normal distributions (KolmogorovSmirnov). Results were found to meet all of these assumptions.

### 69 Weibull distribution

70 Survivorship data for populations may be compared using the Weibull 71 frequency distribution (Weibull, 1939; Pinder et al., 1978). The Weibull 72 frequency distribution is widely used in engineering as a component time to 73 failure model and is considered an appropriate model of animal survivorship 74 (Pinder et al., 1978). The distributions of the survivorship data were fitted to 75 the Weibull distribution using least sum of squares linear regression and the fit 76 was tested with an ANOVA. For distributions that fit the Weibull distribution 77 (ANOVA, p<0.05) the Weibull shape parameter ( $\beta$ ) was determined from the 78 slope of the regression line. The parameter may take several forms: If  $\beta > 1$ 79 individuals probability of mortality increases with age; if  $\beta < 1$  the probability of 80 mortality decreases with age; and if  $\beta = 1$  there is a constant probability of 81 death. The Weibull shape parameter was used to compare survivorship 82 patterns between bivalve populations (Fig. DR3).

## 83 2. Additional details on statistical results

Bivalve size data were compared using non-parametric statistical tests (Tables DR2 and DR3). Median shell size of both species significantly differed between populations (*p*<0.001: Table DR2). *Post hoc* comparisons of

87 individual populations were made using critical values and significant 88 differences are shown on Fig. DR3. Median shell size significantly differed 89 (p < 0.001) between data when grouped into Interval 2 and Interval 3, and between data grouped into periods of increasing and decreasing  $\delta^{13}C_{ora}$ 90 91 (Table DR3). 92 Linear regressions were performed with raw, 3 point moving average, 93 and per ~75cm Milankovitch cycle averaged bivalve size data (Table DR4). All 94 correlations were significant (p<0.005) and the strongest relationships were 95 found for size data averaged per 75 cm Milankovitch cycle (equivalent to precession or obliquity). Stronger coefficients of determination were found for 96 97 maximum rather than mean shell size because it is less variable (Table DR4). 98 Linear regressions of *P. dubius* shell size were performed with 99 geochemical proxies for seawater temperature ( $\delta^{18}$ O and Mg/Ca; Bailey et al., 2003) and paleoproductivity ( $\delta^{15}$ N; Jenkyns et al., 2001) that are predicted to 100 101 influence bivalve shell size directly or indirectly (e.g. the impact of seawater temperature change on paleoproductivity; Gomez and Goy, 2011). However, 102 103 these regressions were not significant (Table DR5). This is highly likely to be 104 a function of the lower stratigraphic resolution of these proxy data.

105

Statistical Test	Test statistic	Significance level (p)	n
P. dubius shell size*			
Kruskal-Wallis	7465	<0.001	186
Jonkheere-Terpstra <sup>†</sup>	27.19	<0.001	186
Median test	5393	<0.001	186
<i>B. radiata</i> shell size <sup>*</sup>			
Kruskal-Wallis	1996	<0.001	35
Jonkheere-Terpstra <sup>†</sup>	10.95	<0.001	35
Median test	1341	<0.001	35

\*Size data are shell surface area (mm<sup>2</sup>) for raw data see Fig. DR 2

<sup>†</sup>Positive values indicate trend is increasing values with stratigraphic height.

1	06
1	07

Statistical Comparison	Test statistic	n	Significance level (p)
<u>B. radiata shell size</u>			
Decreasing versus Increasing $\delta^{13}C_{\text{org}}$	-9.99	6162	<0.001
<u>P. dubius shell size</u>			
Interval 2 versus Interval 3	-27.85	29673	<0.001
Note: tests compare medians; n = sam	ple size; p<0.05 ir	ndicates sig	nificant difference.
<sup>*</sup> Size data are shell surface area (mm <sup>2</sup>	)		

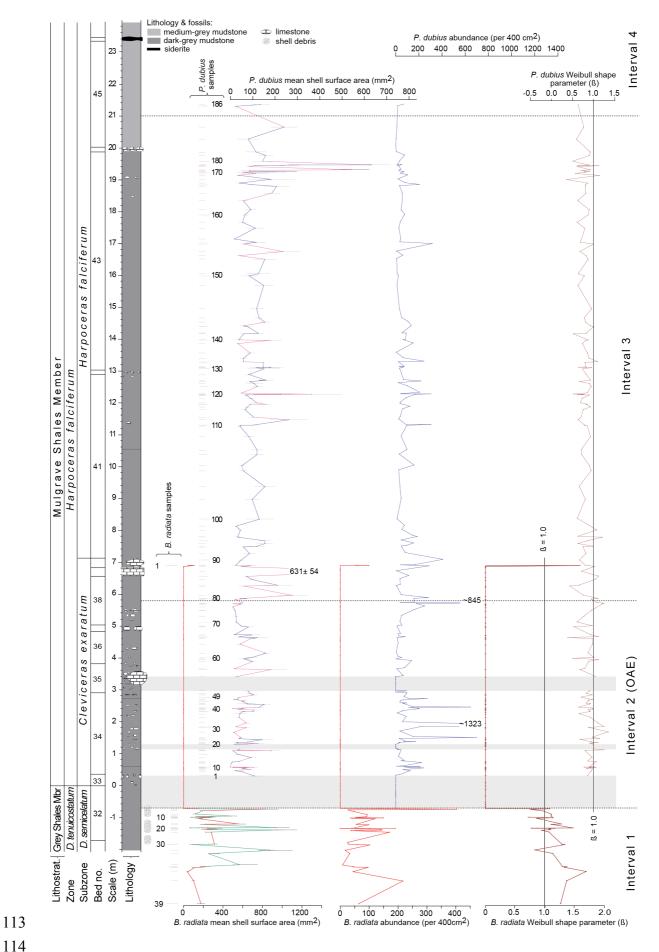
#### TABLE DR4. RESULTS OF LINEAR REGRESSIONS FOR P. dubius SIZE

Proxy	Coefficient of determination						
	Mean shell surface area		Mean shell surface		Ν	/lax shell surf	ace area
	Raw	3 pt.	Mkv.	Raw	3 pt. ma	Mkv. av.	
[Mo]	0.10	0.27	0.39	0.18	0.36	0.62	
$\delta^{98/95} Mo$	0.12	0.27	0.37	0.16	0.29	0.40	
TOC/P	0.09	0.25	0.32	0.11	0.20	0.38	
n	185	93	35	185	93	35	
Note: all	significan	t at <i>p&lt;</i> 0.00	5; Mk. av.	= Milanke	ovitch averag	e; 3 pt. ma =	
3 point mo	oving avera	age; n = sa	mple size.				

TABLE DR5. RESULTS OF REGRESSION OF P. dubius SIZE WITH OTHER PROXIES

Geochemical proxy	R <sup>2</sup>	R <sup>2</sup> Significance level (p)		
N-isotopes (δ <sup>15</sup> N)	0.076	0.386		
O-isotopes ( $\delta^{18}$ O)	0.100	0.142		
Mg/Ca	0.014	0.581		

#### Caswell and Coe: Data repository item 2013XXX



115 Figure DR3 (previous page). Stratigraphic log for part of the Toarcian of Yorkshire showing 116 mean shell surface area (with 95% CI), shell abundance (within 400 cm<sup>2</sup>), and ß the Weibull 117 shape parameter for *P. dubius* (blue and pink lines; the pink part indicating significantly 118 different medians of the two adjacent points) and B. radiata (red and green lines with the 119 green part indicating significantly different medians). For the Weibull shape parameter 10 of 120 the 221 stratigraphic levels are not plotted because ß could not be calculated. Data are from 121 the 221 stratigraphic levels sampled; sample points are numbered 1-186 for P. dubius (level 122 50 does not exist) and 1-39 for B. radiata (levels 17, 24 and 25 do not exist). Stratigraphic log 123 from Kemp et al. (2005) and Kemp (2006); ammonite zones and bed numbers from Howarth 124 (1992). Dashed black horizontal lines show the position of intervals 1-4 of Pearce et al. 125 (2008); horizontal gray bands indicate the very poorly fossiliferous intervals (Caswell et al. 126 2009). Ammonite subzones: D. tenuico. = Dactylioceras tenuicostatum Subzone; D. semi. = 127 D. semicelatum Subzone.

128 **3. Background to** *Mulinia lateralis* a modern analogue for

## 129 **Pseudomytiloides dubius**

130 Mulinia lateralis (Say) is a small (~15 mm shell length; e.g. fig. 13, Pl. 131 24 of Tunnell et al. (2010) and Rosenberg (2013)) widely distributed shallow 132 infaunal suspension-feeding bivalve that appears, based on our study, to be a 133 good modern analogue for P. dubius. Mulinia lateralis inhabits soft muddy 134 substrates similar to those inferred for P. dubius during the Toarcian. Mulinia 135 lateralis occurs in high abundances in anoxic conditions in areas such as 136 Chesapeake Bay (Dauer et al., 1992), and Long Island Sound, USA (Sanders, 1956) where densities of up to 21,000 individuals per m<sup>-2</sup> have been reported 137 (Santos and Simon, 1980). This is comparable to P. dubius that we record at 138 densities up to 12.500 individuals per  $m^2$ . Occurrences of *M. lateralis* are 139 140 sporadic and its distribution shows large spatial and temporal variation (e.g. it 141 is observed in very high densities one year but absent the next) (Sanders, 142 1956; Levinton, 1970; Holland et al., 1977). This distribution pattern has been 143 identified for several highly opportunistic species from the geologic record (Levinton, 1970). The present study shows that abrupt large shifts in the size 144 145 of *P. dubius* populations occurred during the Toarcian OAE, and suggests that P. dubius was also highly opportunistic and could rapidly respond to 146 147 favourable environmental conditions. 148 *Mulinia lateralis* is an opportunist that is able to colonise areas rapidly

because it has very fast growth rates and generation times (as short as 60

150 days; Calabrese, 1970) and high fecundity ~3-4 million eggs produced per

151 female (Calabrese, 1969). The population structure of *P. dubius* (Fig. DR5)

and *M. lateralis* (Fig. DR4B) are indicative of high recruitment and juvenile
mortality, and thus for *P. dubius* it is likely that generation times were also
fast. This life history would have enabled *P. dubius* to colonise the seafloor
rapidly when palaeoenvironmental conditions became suitable. Several
factors influence bivalve growth including food supply, temperature, salinity,
and oxygen; and of these the most important is food supply (e.g. Gosling,
2003).

159 Some extant bivalves that inhabit anoxic environments have 160 chemosymbionts, e.g. the Mytilidae, Solemyidae, Lucinidae, Thyasiridae and 161 Vesicomyidae. Determining whether an extinct species had chemosymbionts 162 is difficult because little evidence is preserved on the shell. Some studies use 163 features on the internal shell surface (Taylor and Glover, 2000) and others use stable isotope composition (e.g. CoBabe, 1991), but the Toarcian bivalve 164 165 shell material is not suitable for these analyses. Although chemosymbiosis 166 cannot be excluded for the Toarcian species this life habit seems highly 167 unlikely because neither of the Toarcian species has modern relatives, below 168 the order level, with adaptations for chemosymbiosis. Additionally, we have 169 shown that the Toarcian bivalves decrease in size and abundance when 170 conditions were at their worst (as shown by the geochemical proxy data; Fig. 171 1) whereas we would predict that if the Toarcian bivalves used 172 chemosymbionts they would be larger and more abundant under these 173 conditions. The present day opportunist *M. lateralis* does not have 174 chemosymbionts but it is well adapted to deoxygenated environments 175 (discussed in detail below). Similar to *M. lateralis* we propose that the 176 Toarcian bivalves had adaptations that enabled them to inhabit deoxygenated 177 environments.

178 Despite its high abundance in anoxic conditions *M. lateralis* has low 179 tolerance to anoxia compared with other bivalve species that inhabit muddy 180 substrates (Shumway et al., 1983). During anoxia, unlike other bivalves that 181 close their valves and decrease their activity to conserve energy *M. lateralis* 182 maintain near normal activity levels and continue to feed (Shumway et al., 183 1983). This requires that they switch to anaerobic metabolism, but this is energetically less efficient and so requires a greater energy supply (Shumway 184 185 and Newell, 1984). *Mulinia lateralis* has high filtration rates ~100 ml h<sup>-1</sup> to

186 support its high energy demands (Shumway and Newell, 1984). Shumway 187 and Newell (1984) suggest that this species is adapted to short term 188 fluctuating anoxia and exploiting conditions where food supply is very high 189 such as during phytoplankton blooms. Unlike other bivalve species *M. lateralis* 190 cannot breakdown stored proteins (Shumway and Newell, 1984), and 191 therefore during periods of low food availability large populations of M. 192 lateralis can no longer be supported, and mass mortalities occur. Chalemwart 193 et al. (1991) showed that *M. lateralis* can efficiently assimilate bacterial 194 biomass, and thus cyanobacteria could constitute an important food source 195 for this species if present in high quantities. Although we cannot study the 196 metabolism of *P. dubius* because it is extinct the relationship we find between 197 N<sub>2</sub>-fixing primary productivity and *P. dubius* body-size in this study strongly 198 suggests it may also have been adapted to exploit cyanobacterial and/or algal 199 blooms under fluctuating anoxia.

Within the high-density Toarcian *P. dubius* populations (Figs 1A–B) competition for resources would have been high, and the body size abundance relationships for *P. dubius* populations indicates that smaller individuals utilised resources more efficiently. A smaller body size may have been advantageous because of the larger surface area to volume ratio. For example, Shumway et al. (1983) showed that small individuals of *M. lateralis* had a larger gill surface area to body size ratio than larger individuals.

207 Shumway et al. (1983) suggested that *M. lateralis* is a poor competitor 208 that only flourishes when other species are absent, and this is attributed to its 209 low tolerance of repeated burial in soft sediments. P. dubius also only occurs 210 in any significant numbers in monospecific pavements during the Toarcian 211 OAE and therefore it appears that it was probably also a poor competitor. It 212 may also, like *M. lateralis*, have required very high food supply and so only 213 occurred where phytoplankton blooms were frequent. Furthermore, P. dubius 214 may have had preference for a particular food source(s) as shown for several 215 present day filter feeding bivalve species by Shumway et al. (1985).

## **4. Additional information on bivalve population structure**

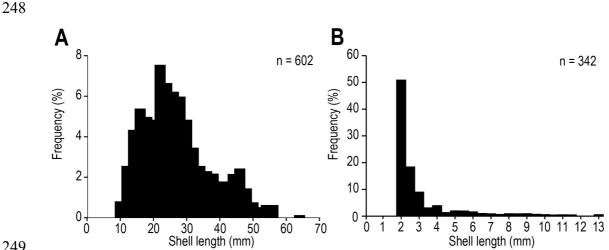
217 Positively skewed size frequency distributions are common for present 218 day marine bivalve populations that broadcast spawn and have high juvenile

219 mortality. However, patterns vary from positively to negatively skewed 220 between different populations. The size structure of two present day 221 suspension feeding bivalve populations, Mya arenaria and Mulinia lateralis 222 are shown (Fig. DR4) for comparison with those from the Toarcian (Figs 223 DR5–7). Both of these present day species inhabit de-oxygenated 224 environments but they have very different life history strategies. 225 Mya arenaria has a deep infaunal life habit within reducing 226 environments where it attains oxygen from the overlying oxygenated seawater 227 via its long siphons. Mya arenaria is considered to have an equilibrium life 228 history strategy (Fig. DR4A). It has a relatively long life span ~20 years and 229 reaches sexual maturity after 2 years. This is reflected by its larger body size 230 and the moderately positively skewed and multimodal population size 231 distribution indicating that multiple cohorts were present (with a modal size of

232 25 mm shell length) and 99% of individuals attained shell lengths greater than233 10 mm (Fig. DR4A).

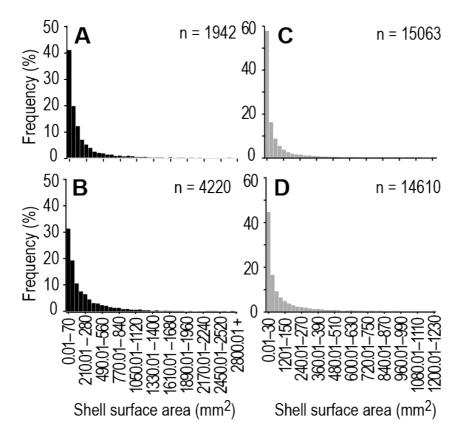
In contrast, *M. lateralis* (discussed in DR Section 3) is an opportunistic species (Fig. DR4B) with a tenfold shorter life span (2 years) and twelvefold faster generation time (2 months) than *M. arenaria*. The size distribution of a time averaged *M. lateralis* population (Fig. DR4B) is strongly positively skewed suggesting high recruitment and juvenile mortality. Only one size cohort exists and less than 50% of individuals in the population attained a shell length greater than 2 mm (Fig. DR4B).

Both Toarcian bivalve species had unimodal strongly positively skewed SFDs (Fig. DR5). Individual *B. radiata* SFDs (i.e. the uncombined SFDs) showed that multimodal distributions were more frequent when  $\delta^{13}C_{org}$  was decreasing within a cycle as opposed to  $\delta^{13}C_{org}$  increasing (Fig. DR7). Additionally, more of the *P. dubius* SFDs (per Milankovitch cycle, Fig. DR6) were multimodal during Interval 3 compared with Interval 2.





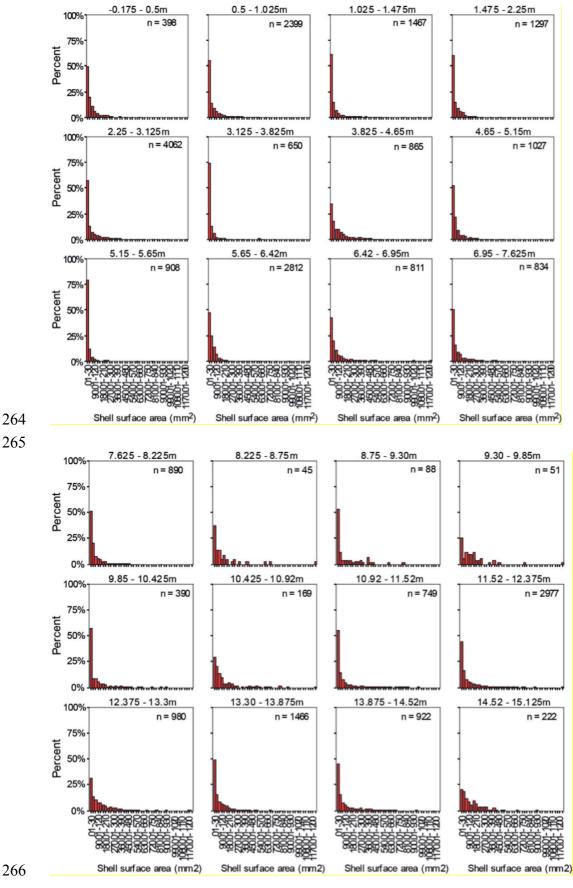
250 Figure DR4. Example length frequency distributions (LFDs) for populations of present day 251 bivalves with equilibrium (A) and opportunistic life histories (B). A: Mya arenaria LFDs 252 compiled from several samples collected intertidally at East Passage, Nova Scotia in 1987 253 (data re-plotted from Emerson et al. (1988)). B: LFD of a time averaged population of Mulinia 254 lateralis collected subtidally from Long Island Sound, Conneticut, USA (data re-plotted from 255 Levinton and Bambach (1970)). The absence of shells < 0.5 mm and 1 mm in length results 256 from the sieve size used for sampling *M. arenaria* and *M. lateralis*, respectively. 257



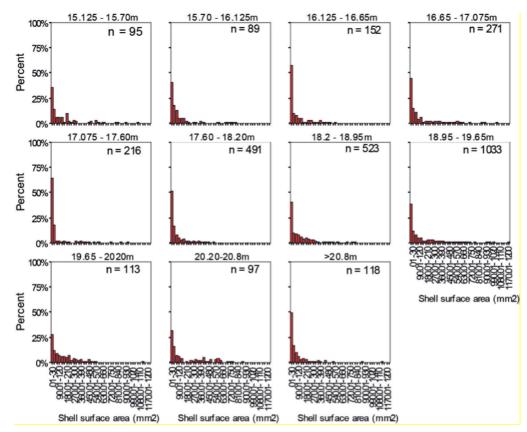
259 Figure DR5. Size frequency distributions for all Toarcian samples within particular

260 stratigraphic levels combined showing percent frequency of shells within 41 size categories.

- 261 A: *B. radiata* (gray) when  $\delta^{13}C_{org}$  are increasing; and B: decreasing. C: *P. dubius* (black) from
- 262 Intervals 2; and D: P. dubius from Interval 3.
- 263

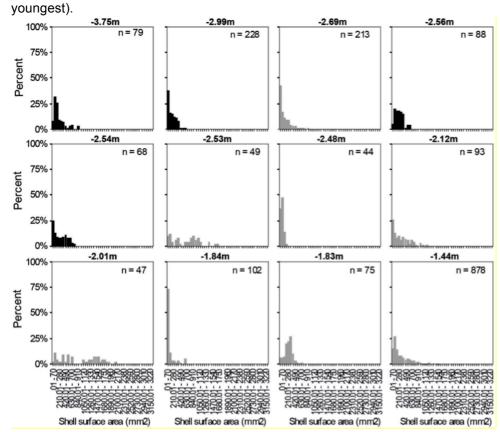






268

Figure DR6. Size frequency distributions of *P. dubius* for data combined per ~75 cm
 Milankovitch cycle. Plots show the percentage of shells in each 30 mm<sup>2</sup> (surface area) size
 category; stratigraphic heights of each Milankovitch cycle are shown (from oldest to
 youngest).



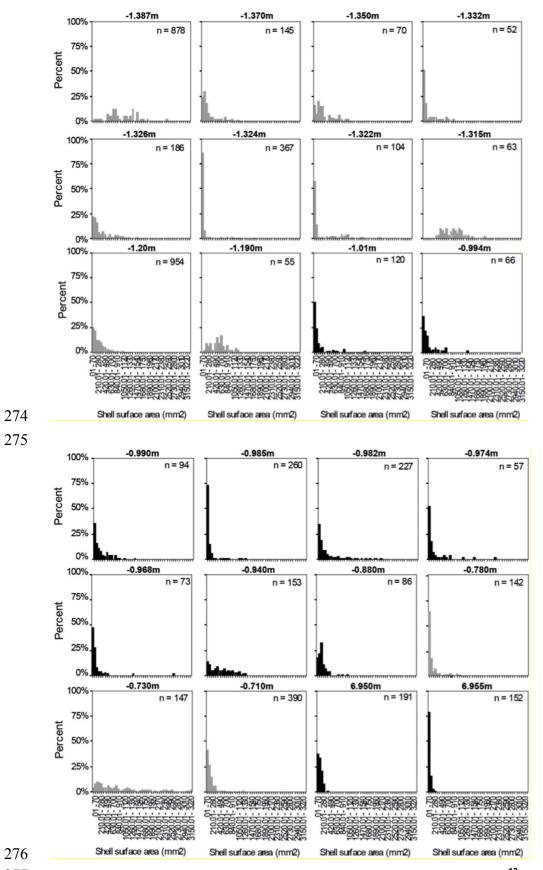


Figure DR7. Size frequency distributions for 36 *B. radiata* populations when  $\delta^{13}C_{org}$  was increasing (black) and when  $\delta^{13}C_{org}$  was decreasing (gray). Plots show percentage of shells in each 70 mm<sup>2</sup> size (surface area) category. Stratigraphic heights (m) are shown for each

280 population (ordered from oldest to youngest).

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