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2 **ISOTOPIC TEMPERATURES FROM THE EARLY AND MID-PLIOCENE**  
3 **OF THE US MIDDLE ATLANTIC COASTAL PLAIN,**  
4 **AND THEIR IMPLICATIONS FOR THE CAUSE OF REGIONAL MARINE**  
5 **CLIMATE CHANGE**

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26

27 ABSTRACT

28

29 Mean seasonal extreme temperatures on the seafloor calculated from the shell  
30  $\delta^{18}\text{O}$  of the scallop *Placopecten clintonius* from the basal part of the early  
31 Pliocene Sunken Meadow Member (Yorktown Formation) in Virginia are very  
32 similar to those from the same horizon at the latitude of Cape Hatteras in North  
33 Carolina (~210 km to the south). The lowest and highest temperatures calculated  
34 from each shell (using  $\delta^{18}\text{O}_{\text{seawater}} = +0.7\text{‰}$ ) give mean values for winter and  
35 summer of  $8.4 \pm 1.1 \text{ }^\circ\text{C}$  ( $\pm 1\sigma$ ) and  $18.2 \pm 0.6 \text{ }^\circ\text{C}$  in Virginia, and  $8.6 \pm 0.4 \text{ }^\circ\text{C}$  and  
36  $16.5 \pm 1.1 \text{ }^\circ\text{C}$  in North Carolina (respective median temperatures:  $13.3 \text{ }^\circ\text{C}$  and  
37  $12.6 \text{ }^\circ\text{C}$ ). Patterns of ontogenetic variation in  $\delta^{18}\text{O}$ ,  $\delta^{13}\text{C}$  and microgrowth  
38 increment size indicate summer water-column stratification in both areas, with  
39 summer surface temperatures perhaps  $6 \text{ }^\circ\text{C}$  higher than on the seafloor. The low  
40 winter paleotemperatures in both areas are most simply explained by the greater  
41 southward penetration of cool northern waters in the absence of a feature  
42 equivalent to Cape Hatteras. The same current configuration but a warmer  
43 general climate can account for the high benthic seasonal range (over  $15.0 \text{ }^\circ\text{C}$  in  
44 some cases) but warmer median temperatures ( $15.7\text{-}21.3 \text{ }^\circ\text{C}$ ) derived from  
45 existing  $\delta^{18}\text{O}$  data from scallops of the higher Yorktown Formation (using  
46  $\delta^{18}\text{O}_{\text{seawater}} = +0.7\text{‰}$  for the upper Sunken Meadow Member and  $\delta^{18}\text{O}_{\text{seawater}} =$   
47  $+1.1\text{‰}$  for the mid-Pliocene Rushmere, Morgarts Beach and Moore House  
48 members). Existing  $\delta^{18}\text{O}$  data from the infaunal bivalve *Mercenaria* of the  
49 Rushmere Member yields a similarly high median temperature ( $21.6 \text{ }^\circ\text{C}$ ) but a  
50 low seasonal range ( $9.2 \text{ }^\circ\text{C}$ ), pointing to the periodic influence of warm currents,  
51 possibly at times when the Gulf Stream was exceptionally vigorous.

52

53

## INTRODUCTION

54

55 The Pliocene (5.33–2.58 Ma) contains the most recent interval (~3.3-3.0 Ma) in  
56 which global mean surface temperature was significantly higher than present (by 1.9-  
57 3.6°C; Masson-Delmotte et al., 2013). This interval – the mid-Pliocene or, more  
58 strictly, mid-Piacenzian Warm Period (both abbreviated to MPWP) – has been the  
59 focus of study for nearly 30 years by the Pliocene Research, Interpretation and  
60 Synoptic Mapping (PRISM) group of the United States Geological Survey (Dowsett  
61 et al., 2016). It has been used extensively as a test-bed for numerical models of an  
62 Earth with relatively high atmospheric CO<sub>2</sub> because concentrations of this greenhouse  
63 gas were well above pre-industrial interglacial values according to most  
64 reconstructions (e.g., Masson-Delmotte et al., 2013; Martínez-Boti et al., 2015), yet  
65 many other large-scale aspects of paleogeography (e.g., continental positions,  
66 orography, ocean current patterns) were similar to now. Model outputs for the MPWP  
67 are consistent with proxy estimates of temperature at the global scale and for many  
68 regions. However, for certain parts of the North Atlantic, proxy estimates are  
69 substantially higher (Dowsett et al., 2012, 2013), indicating either inadequacies in the  
70 models (including the boundary conditions used) or the proxy data. At some relatively  
71 high-latitude (>45 °N) sites in the North Atlantic, congruent evidence of substantial  
72 warming (mean annual sea surface temperature >5 °C above present) is available from  
73 multiple proxies (foraminiferal assemblage composition, foraminiferal Mg/Ca ratios  
74 and alkenone unsaturation index; Dowsett et al., 2012), suggesting that it is the model  
75 estimates that are inaccurate. The high-latitude warmth has been ascribed (e.g.,  
76 Dowsett et al., 1992; Cronin and Dowsett, 1996) to stronger northward transfer of

77 heat by ocean currents than now, but model outputs do not support this (Fedorov et  
78 al., 2013; Zhang et al., 2013).

79       Enhanced ocean transport of heat during the Pliocene has also been inferred from  
80 proxy temperature data for lower latitudes in the North Atlantic region, on the Middle  
81 Atlantic Coastal Plain of the USA. At present, mean winter minimum and mean  
82 summer maximum sea surface temperatures lie in the ranges 5.0-10.0 °C and 22.5-  
83 27.5 °C, respectively, at coastal to outer shelf locations off northern North Carolina  
84 (north of Cape Hatteras) and Virginia (Table 1, stations ORIN7, DUCN7, 44006,  
85 44014, CHLV2, CBBV2, KPTV2, OCIM2, 44009). However, during deposition of  
86 the upper (Rushmere, Morgarts Beach and Moore House) members of the Pliocene  
87 Yorktown Formation, biotic assemblage evidence (see below) points to much warmer  
88 conditions in this area: specifically, winter minimum temperatures above 10 °C.  
89 Greater warmth north of Cape Hatteras during the interval concerned, which overlaps  
90 the MPWP (Fig. 1), has been ascribed to more vigorous northward flow of warm  
91 currents, supplying more heat (Cronin and Dowsett, 1996; Knowles et al., 2009;  
92 Williams et al., 2009; Winkelstern et al., 2013). However, Ward et al. (1991)  
93 attributed the greater warmth simply to higher sea level and the absence of a barrier  
94 equivalent to modern Cape Hatteras, allowing free passage of warm waters  
95 northwards across the shelf. If this explanation is correct, it has implications not only  
96 for our understanding of the northward expansion of warm conditions on the Atlantic  
97 Coastal Plain but also in the wider North Atlantic: elevated temperatures at higher  
98 latitudes might reflect a more northward trajectory rather than increased strength of  
99 warm-current flow. However, both of these explanations would be called into  
100 question if the higher temperatures recognised north of Cape Hatteras are not the

101 result of greater warm-current influence but of generally warmer conditions, caused  
102 by some other factor (e.g., increased atmospheric CO<sub>2</sub>).

103 We attempt to identify the cause of mid-Pliocene warming north of the latitude of  
104 Cape Hatteras using estimates of seasonal marine paleotemperature from the oxygen  
105 isotopic ( $\delta^{18}\text{O}$ ) composition of bivalve shells from the Yorktown Formation. Most of  
106 the data derives from scallops, which are a propitious subject because in early  
107 ontogeny they typically grow rapidly and throughout the year, thus preserving an  
108 easily recoverable record of the full range of seasonal temperature variation (e.g.,  
109 Johnson et al., 2009; Chute et al., 2012), and kinetic and ‘vital’ effects seem to be at  
110 most small (e.g., Barrera et al., 1990; Hickson et al., 1999; Owen et al., 2002a, b). In  
111 addition, most scallops live only in fully marine conditions, thus reducing  
112 uncertainties about the value to use for  $\delta^{18}\text{O}_{\text{seawater}}$  in the isotopic temperature  
113 equation. We present new data from the genus *Placopecten* of the early Pliocene  
114 Sunken Meadow Member in Virginia and North Carolina, using this to formulate a  
115 model of climate and water circulation for a time when coastline geometry was much  
116 like that in the mid-Pliocene (i.e., no ‘Cape Hatteras’) yet sea temperatures were  
117 lower according to independent evidence. We then derive a prediction for benthic  
118 seasonal temperature range if the subsequent warming of marine climate in the area  
119 was due to an increase in the influence of warm currents. We test this hypothesis  
120 through a reanalysis of existing  $\delta^{18}\text{O}$  data from other scallops (*Chesapecten* and  
121 *Carolinapecten*) of the Yorktown Formation, both from a horizon in the Sunken  
122 Meadow Member above that of the *Placopecten* shells and from all three of the higher  
123 (mid-Pliocene) members of the Yorktown Formation. Finally, we review existing  
124 mid-Pliocene isotopic temperature data from the infaunal (non-scallop) bivalve  
125 *Mercenaria* and estimates of mid-Pliocene seasonal temperature range from bryozoan

126 zooid-size variation, identifying and attempting to explain discrepancies with the  
127 scallop data and then making recommendations for further research. Since all the data  
128 discussed is in the form of ontogenetic or astogenetic profiles from mineralised,  
129 accretionarily-produced skeletal material, the investigation constitutes a case-study in  
130 sclerochronology (Schöne and Gillikin, 2013).

131

132 ISOTOPIC TEMPERATURES FROM *PLACOPECTEN CLINTONIUS* OF THE  
133 BASAL SUNKEN MEADOW MEMBER

134

135 Background Information

136

137 *Stratigraphy.*—The Sunken Meadow Member is the lowermost of the four  
138 members constituting the Yorktown Formation (Fig. 1), occurring in southeast  
139 Virginia and northeast North Carolina and averaging about 3 m thick. It mainly  
140 consists of fine-grained quartz sands, but towards the west the basal part is a medium  
141 to coarse sand (with a coarse lag deposit at the very base), while the finer deposits to  
142 the east are glauconitic in the north and phosphatic in the south; an abundant and  
143 diverse marine fauna occurs throughout (Ward and Blackwelder, 1980; Ward et al.,  
144 1991). Evidence of coeval marine sedimentation extending into South Carolina exists  
145 in the form of lag deposits at the base of younger units (Ward et al., 1991). Other  
146 marine deposits present farther south and considered to be of approximately the same  
147 age are ‘Unit 11’ of the lower Tamiami Formation, which occurs in southwest Florida  
148 (Williams et al., 2009), and the Wabasso Formation, which occurs in the subsurface  
149 of eastern Georgia (Huddleston, 1988). The latter falls within planktonic foraminiferal  
150 biozone PL1 (of Berggren, 1973), which is dated at 4.9-3.7 Ma. The Sunken Meadow

151 Member itself is generally placed (e.g., Dowsett and Wiggs, 1992) within planktonic  
152 foraminiferal biozone N19 (of Blow, 1969), which is dated at 4.8 to ~3.5 Ma  
153 (essentially within the Zanclean) in the calibration of Berggren et al. (1985). Krantz  
154 (1991) tentatively suggested a more precise date of 4.5-4.4 Ma for the Sunken  
155 Meadow Member by relating the transgression associated with its deposition to a  
156 phase of warming and global ice-volume reduction identified in the deep-ocean  $\delta^{18}\text{O}$   
157 record (more fully and recently documented by Lisiecki and Raymo, 2005). The  
158 transgression was preceded by a phase of non-deposition or erosion (associated with a  
159 sea-level lowstand), such that the Sunken Meadow Member rests unconformably on  
160 either the Cobham Bay Member of the Eastover Formation, whose age is no younger  
161 than ~4.9 Ma (Krantz, 1991), or on the Miocene Pungo River Formation (Ward and  
162 Blackwelder, 1980).

163

164 *Hydrography.*—The transgression associated with the Sunken Meadow Member  
165 pushed the coastline up to 150 km west of its present position in southeast Virginia  
166 and northeast North Carolina (Ward et al., 1991; Krantz, 1991). Figure 2B shows its  
167 position according to Ward et al. (1991, fig. 16-4A). If Pliocene non-marine deposits  
168 in Maryland and Delaware correlate with the Sunken Meadow Member, the coastline  
169 may have been somewhat farther south in this area, nearer the Virginia state line, as  
170 reconstructed by Pazzaglia (1993). In a seismic study in eastern Albemarle Sound,  
171 North Carolina (north of Cape Hatteras), Mallinson et al. (2005) identified south- to  
172 southwestward-dipping clinoforms within lower Pliocene clastic sediments. They  
173 considered that these might represent a delta advancing from the northeast (implying  
174 that the coastline was recurved southward to this area) but also accepted that they  
175 might represent advancing shelf bedforms, an interpretation supported by

176 foraminiferal evidence from the adjacent Mobil#1 well (Zarra, 1989). The eastward  
177 fining within the Sunken Meadow Member mentioned above is inconsistent with the  
178 existence of a delta advancing from the northeast but in full agreement with the  
179 position inferred by Ward et al. (1991) for the Sunken Meadow coastline in northern  
180 North Carolina (Fig. 2B). Farther south, the Mid-Carolina Platform High (centred on  
181 the North/South Carolina state line and a persistent influence on Cenozoic  
182 sedimentation; Riggs and Belknap, 1988) probably caused a reduction in water depth,  
183 but the lag deposits referred to above argue against emergence. The coastline  
184 therefore lay some distance inland of its present position (Fig. 2B). In summary, while  
185 the exact form of the coastline during Sunken Meadow deposition may have differed  
186 slightly from the configuration in Figure 2B, its shape was only mildly curvilinear,  
187 lacking an eastward protrusion as large as modern Cape Hatteras (whose tip lies in  
188 North Carolina at  $\sim 35^{\circ}\text{N}$ , some 140 km south of the North Carolina-Virginia state  
189 line). Consequently neither northward- nor southward-flowing currents would have  
190 been deflected to the east as they are now (Fig. 2A).

191       At present, the Gulf Stream is a very warm and rapid western boundary current  
192 flowing northward above the Florida-Hatteras Slope to Cape Hatteras, where it  
193 diverges from the continental margin. Closer to the coast (on the shelf) current flow  
194 is weaker and more variable in direction, but still generally towards the north  
195 (Bumpus, 1973; Atkinson et al., 1983). This flow has been termed the Carolina  
196 Coastal Current (Cronin, 1988). At times surface intrusions from the Gulf Stream  
197 bring very warm water onto the North Carolina shelf south of Cape Hatteras  
198 (Atkinson, 1977). Farther south in the South Atlantic Bight (SAB; Cape Hatteras to  
199 Cape Canaveral) there also occur intrusions of deeper, relatively cool (and more  
200 nutrient-rich) Gulf Stream water onto the shelf, but these are relatively infrequent in

201 the northern SAB (Atkinson et al., 1983). In the southern part of the Middle Atlantic  
202 Bight (MAB; Cape Hatteras to Cape Cod), there is typically a weak southward flow  
203 on the shelf (Bumpus, 1973), termed the Virginia Coastal Current (Cronin, 1988).  
204 This is approximately paralleled by a similar surface current above the upper and  
205 middle zones of the continental slope, in the western part of the Slope Sea between  
206 the shelf and Gulf Stream (Csanady and Hamilton, 1988; Böhm et al., 2006).

207 In the absence of a feature analogous to Cape Hatteras during Sunken Meadow  
208 deposition, it is reasonable to assume that there was no region of very steep latitudinal  
209 gradient in sea-surface temperature (SST) as there is now adjacent to the Cape  
210 because of the meeting of warm northward-flowing and cool southward-flowing  
211 water. However, even if the Gulf Stream was as strong as at present (suggested by  
212 evidence of early Pliocene submarine erosion on the Florida-Hatteras Slope; Pinet and  
213 Popenoe, 1985), it is not certain that warm water would have extended north into the  
214 area of present-day Virginia. The main current might still have turned eastwards, in  
215 the manner of all western boundary currents at 30-40° from the equator, so surface  
216 intrusions onto the Virginia shelf would have been rare. Also, any equivalent of the  
217 Carolina Coastal Current might not have been strong enough to displace cool  
218 southward-flowing waters, given that with the present coastal configuration northern  
219 shelf waters penetrate as far south as Cape Fear (Fig. 2B) about 10% of the time  
220 through wind-forcing (Pietrafesa et al., 1994). In fact, the Gulf Stream may have been  
221 less strong than now (i.e., more like the Brazil Current and East Australian Current,  
222 which are relatively weak western boundary currents) during deposition of the Sunken  
223 Meadow Member, due to incomplete development of the Central American Isthmus  
224 (Cronin and Dowsett, 1996; Schmidt, 2007). Hence, supply of warm water by currents  
225 into the area of present-day Virginia is still less certain. Ward and Blackwelder (1980)

226 considered that at this time a structural high in the area of Cape Fear (essentially part  
227 of the Mid-Carolina Platform High) was sufficiently elevated to prevent northward-  
228 flowing warm waters entering the area of deposition of the Sunken Meadow Member,  
229 and Cronin and Dowsett (1996) took the view that the shelf off the eastern US was  
230 influenced only by southward-flowing cool currents in the early Pliocene.

231 Ward et al. (1991) considered that deposition of the Sunken Meadow Member took  
232 place in mid-shelf water depths of 20-40 m under the influence of upwelling (from the  
233 evidence of glauconite and phosphate). Purdy et al. (2001) and Fierstine (2001) also  
234 inferred upwelling but greater water depths (>50 m and >100m, respectively) from the  
235 fish fauna. The generally fine-sand sediments suggest neither strong wave action nor  
236 vigorous tidal currents, so it is possible that there was significant thermal stratification  
237 of the water column in summer, as now at similar latitudes and depths off eastern  
238 North America. For instance, at 30 m depth in the modern MAB (at approximately the  
239 latitude of the North Carolina-Virginia state line), water temperature is about 6 °C less  
240 than at the surface in summer (Winkelstern et al., 2013). Spring freshwater run-off  
241 (reducing the salinity and hence density of surface waters) assists this stratification  
242 but also causes a temporary reduction in the salinity of bottom waters (from about  
243 34.5 psu to 32.5 psu) as far offshore as the outer shelf (Krantz et al., 1988, fig. 1). In  
244 the modern SAB, bottom salinity is somewhat higher and essentially constant (at  
245 about 36 psu) through the year (Krantz et al., 1988, fig. 1). It is difficult to determine  
246 from first principles whether, in the absence of a feature analogous to Cape Hatteras,  
247 the area of deposition of the Sunken Meadow Member would have more resembled  
248 the modern MAB or SAB in respect of the influence of freshwater run-off. However,  
249 it seems improbable that there were significant differences over the area of deposition.

250

251 *Marine Climate*.—The classification of terrestrial climates has been extensively  
252 discussed and several schemes have been developed (e.g., ‘Köppen-Geiger’,  
253 ‘Köppen-Trewartha’; Belda et al., 2014), with each climate defined by precise  
254 criteria. Marine climate (usually considered in terms of seasonal minimum and  
255 maximum temperatures in surface or shallow subsurface waters) has received less  
256 attention and the divisions recognised have been poorly and differently defined. For  
257 ‘inner sublittoral’ bottom waters of the modern eastern US shelf, Hazel (1971, 1988)  
258 recognised a ‘mild temperate’ marine climate north of Cape Hatteras (to 38 °N, and  
259 by implication to beyond 39 °N), defined by winter minimum temperatures in the  
260 range 2.5-5.0 °C and summer maximum temperatures in the range 20.0-22.5 °C.  
261 Winter minimum surface temperatures are actually higher than 5 °C (though less than  
262 10 °C) at coastal to outer shelf locations up to 180 km north of Cape Hatteras (Table  
263 1, stations ORIN7, DUCN7, 44006, 44014, CHLV2, CBBV2) and at depths of a few  
264 tens of metres temperatures are probably a degree or two warmer (though still less  
265 than 10 °C; Winkelstern et al., 2013). Summer maximum surface temperatures exceed  
266 22.5 °C in this area and farther north (Table 1) but at a few tens of metres depth they  
267 may be within the range for a mild temperate climate given by Hazel (1971, 1988), or  
268 even the redefined range given by Krantz (1990; 17.5-20.0 °C), due to thermal  
269 stratification (Winkelstern et al., 2013). Hazel (1971, 1988) recognised a ‘subtropical’  
270 marine climate at present immediately south of Cape Hatteras (to 35 °N, and by  
271 implication to beyond 33 °N), defined by winter minimum and summer maximum  
272 temperatures in the ranges 12.5-15.0 °C and 27.5-30.0 °C, respectively. His diagrams  
273 (1971, fig. 6; 1988, fig. 8) belie the figures given for summer maximum temperature,  
274 suggesting a range of 25.0-27.5 °C. This is the range given by Krantz (1990) for  
275 summer maximum temperature in a subtropical marine climate (with temperatures

276 approaching 30 °C in shallow water), and the summer maximum surface temperature  
277 at a mid-shelf location about 8 km south of the latitude of Cape Hatteras (27 °C:  
278 Table 1, station DSLN7) is in agreement with this, as is the winter minimum surface  
279 temperature at this location (15 °C) with the winter minimum range given by Hazel  
280 (1971, 1988) for a subtropical marine climate. Farther south (to beyond 33 °N),  
281 summer maximum surface temperature is in the range 27.5-30.0 °C, even at offshore  
282 locations, and winter minimum surface temperature is below 12.5 °C at most coastal  
283 locations and above 15 °C at most offshore locations, resulting in a much smaller  
284 seasonal range offshore than is seen anywhere north of Cape Hatteras (Table 1). Ward  
285 et al. (1991) termed the modern marine climate north of Cape Hatteras ‘cool  
286 temperate’ but were in agreement with Hazel (1971, 1988) that the ‘subtropical’ zone  
287 to the south is not separated by a zone of ‘warm temperate’ conditions, characterised  
288 by Krantz (1990) as having winter minimum and summer maximum temperatures in  
289 the ranges 10.0-12.5 °C and 22.5-25.0 °C, respectively. Such a zone has, however,  
290 been recognised in southeast Virginia and northeast North Carolina during deposition  
291 of the upper (Rushmere, Morgarts Beach and Moore House) members of the  
292 Yorktown Formation (see below). By contrast, mollusk assemblages indicate a cool  
293 (= mild) temperate marine climate in this area during deposition of the underlying  
294 Sunken Meadow Member (Ward et al., 1991). Ostracod assemblages (Hazel 1971,  
295 1988) support this in the sense that the summer maximum temperatures implied (no  
296 higher than 20 °C) are within the redefined range given by Krantz (1990) for a mild  
297 temperate marine climate. However, the winter minimum temperatures implied (no  
298 lower than 12.5 °C) are above the range for a mild temperate marine climate, and  
299 Hazel (1988) described the marine climate represented by the ostracod assemblages as  
300 warm temperate. Existing isotopic ( $\delta^{18}\text{O}$ ) temperatures for the Sunken Meadow

301 Member (Krantz, 1990) support a mild temperate designation, maximum values (from  
302 profiles exhibiting a summer) being within the redefined range given by Krantz  
303 (1990) and minimum values being within the expanded range described above. The  
304 temperature estimates of Krantz (1990) are considered further below in the light of  
305 research into the oxygen-isotopic composition of ambient water.

306

307

## Materials and Methods

308

309 We used complete and apparently pristine valves of *Placopecten clintonius* (Fig.  
310 3A) from the basal 30 cm of the Sunken Meadow Member (L.W. Ward, personal  
311 communication, 2011). Four specimens from locations on the James River, Virginia,  
312 were provided from the collections of the Virginia Museum of Natural History: three  
313 (VA1, VA2, VA4; VMNH 93624, 93625, 93626, respectively) from Grove Wharf (1  
314 in Fig. 2B) and one (VA3; VMNH 93627) from Claremont (2 in Fig. 2B), which lies  
315 just upstream of the Sunken Meadow type locality (Ward and Blackwelder, 1980).  
316 Two specimens from Lee Creek Mine, North Carolina (3 in Fig. 2B), were collected  
317 by A.L.A. Johnson (NC1, NC2; University of Derby, Geological Collections, 53346,  
318 53347, respectively) and a further two specimens from this location were provided  
319 from the collections of the Florida Museum of Natural History (NC3, NC4; UF  
320 261869, 261868, respectively). Lee Creek Mine is about 210 km south of the Virginia  
321 locations.

322 After washing the valves in tap-water to remove  $\text{NH}_4\text{Cl}$  (see below) and cleaning  
323 following the method adopted by Valentine et al. (2011), a hand-held drill with a 0.5  
324 mm bit was used to extract samples of calcite powder from the outer layer, starting  
325 from a position near the dorsal margin (umbo) and continuing to the ventral margin,

326 except in VA4 (sampled only to 56 mm of the total height of 62 mm) and NC4  
327 (sampled only to 60.5 mm of the total height of 110 mm). Grooves 0.1-0.5 mm in  
328 depth and 5-60 mm in length were cut parallel to microgrowth-increment boundaries  
329 (Fig. 3B) in order to yield sufficient material for analysis and possible repeat analysis.  
330 Samples from VA1, VA2, NC1 and NC2 were extracted at height intervals averaging  
331 1.3-1.5 mm ('fine' sampling) and analysed at the Stable Isotope Facility, British  
332 Geological Survey, Keyworth, using an Isoprime dual inlet mass spectrometer  
333 coupled to a Multiprep system. Powder samples were dissolved with concentrated  
334 phosphoric acid in borosilicate wheeton vials at 90 °C. Samples from VA3, VA4,  
335 NC3 and NC4 were extracted at height intervals averaging 2.3-2.5 mm ('coarse'  
336 sampling) and analysed at the Institute of Geological Sciences, University of Mainz,  
337 using a Thermo Finnigan MAT 253 continuous flow-isotope ratio mass spectrometer  
338 coupled to a Gasbench II. Powder samples were dissolved with concentrated  
339 phosphoric acid in helium-flushed borosilicate exetainers at 72 °C. Both laboratories  
340 calibrated their  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  data against NBS-19 and their own Carrara marble  
341 standard. Internal precision ( $1\sigma$ ) for both laboratories are  $<0.05$  for  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ .  
342 Isotope values were calculated against the Vienna Pee Dee Belemnite (VPDB), Craig  
343 corrected, and reported in delta notation and given as parts per mil (McKinney et al.,  
344 1950).

345 The living descendant of *P. clintonius*, *P. magellanicus*, is a stenohaline marine  
346 form which has been shown to yield accurate information on seasonal temperatures  
347 from  $\delta^{18}\text{O}$  of serial ontogenetic samples (Krantz et al., 1984; Tan et al., 1988; Chute et  
348 al., 2012). In conformity with the work on *P. magellanicus*, temperatures were  
349 calculated using the equation for calcite (1) of Epstein et al. (1953).

350

351 
$$T = 16.5 - 4.3(\delta^{18}\text{O}_{\text{calcite}} - \delta^{18}\text{O}_{\text{seawater}}) + 0.14(\delta^{18}\text{O}_{\text{calcite}} - \delta^{18}\text{O}_{\text{seawater}})^2 \quad (1).$$

352

353 Values for  $\delta^{18}\text{O}_{\text{seawater}}$  (measured against VSMOW) must be adjusted downward  
354 for correspondence with the VPDB scale used for  $\delta^{18}\text{O}_{\text{calcite}}$ . An adjustment of 0.22‰  
355 was used by Chute et al. (2012) in recent work on *P. magellanicus*. However, the  
356 internationally agreed figure is 0.27‰ (Gonfiantini et al., 1995), and this has been  
357 used herein, in conformity with recent work on Pliocene *Mercenaria* from the Middle  
358 Atlantic Coastal Plain (Winkelstern et al., 2013). Various initial values of  $\delta^{18}\text{O}_{\text{seawater}}$   
359 were used in accordance with the differing estimates available (see below).

360 Before the cleaning and isotopic sampling procedure outlined above, the valves  
361 were coated with a sublimate of  $\text{NH}_4\text{Cl}$  (which enhances the visibility of surface  
362 details) and digitally photographed. Images were then imported into the measurement  
363 software Panopea© (2004, Peinl and Schöne) and both the position (shell height) of  
364 growth breaks and the size of microgrowth increments (Fig. 3B) determined along the  
365 axis of maximum growth, except in the umbonal region where (to varying heights) the  
366 record of growth had been effaced by abrasion. Microgrowth-increment profiles  
367 appear to offer insights into the degree of mixing of the water column and therefore  
368 assist interpretation of oxygen-isotope temperature data from bivalves: specifically,  
369 whether or not summer values correspond to surface temperatures or are an  
370 underestimate as a result of the development of thermal stratification (Johnson et al.,  
371 2009). While benthic temperature data is useful in its own right, informed estimation  
372 of the corresponding surface temperature is worthwhile for comparison with model  
373 outputs.

374

375

## Results

376

377 *Oxygen Isotopes.*—Nearly all  $\delta^{18}\text{O}$  values (Fig. 4) are positive and, as expected,  
378 show cyclic patterns in the case of every shell, assumed to reflect seasonal  
379 temperature variation. There is some fairly low amplitude ‘noise’ (e.g., from about  
380 30-50 mm in VA3 and 20-40 mm in NC2; Fig. 4C, 4F), possibly reflecting the local  
381 occurrence of cement-lined micro-borings, as identified in Pliocene *Aequipecten*  
382 *opercularis* (Johnson et al., 2009). Only a few major anomalies are evident. VA3 (Fig.  
383 4C) shows two extremely low values at the end of ontogeny which are very different  
384 from adjacent values and more than 1‰ lower than the minimum value of the  
385 preceding summer in this shell and all summer minima in other shells. VA4 (Fig. 4D)  
386 shows a single-point positive excursion of similar magnitude at a shell height of 16  
387 mm. The anomalous  $\delta^{18}\text{O}$  values in VA3 and VA4 are not accompanied by anomalous  
388  $\delta^{13}\text{C}$  values, but in NC2 (Fig. 4F) a single-point positive excursion of about 1‰ in  
389  $\delta^{18}\text{O}$  at 43.8 mm is matched by a slightly smaller one in  $\delta^{13}\text{C}$ . The values shown for  
390 NC2 are the result of resampling over a zone from 41.7-53.9 mm shell height after  
391 similar anomalies had been identified in the original profiles. Re-detection rules out  
392 contamination or instrumental malfunction. Diagenesis is an unlikely explanation  
393 (also for the anomalously high  $\delta^{18}\text{O}$  value from VA4) because this typically causes a  
394 reduction in  $\delta^{18}\text{O}$  (Tucker and Wright, 1990), but may account for the anomalously  
395 low values from VA3. The lack of concomitant shifts in  $\delta^{13}\text{C}$  in VA3 could reflect the  
396 generally low amount of carbon (relative to oxygen) in porewaters (Tucker and  
397 Wright, 1990). Whatever their cause, it is appropriate to exclude from further analysis  
398 all the above values (signified by stars in Fig. 4). Abrupt excursions to lower  $\delta^{18}\text{O}$   
399 values in the late ontogeny (shell height >80 mm) of the large specimens NC1 and  
400 NC2 (Fig. 4E, 4F, respectively) might be thought to represent anomalies. However,

401 comparison with the large set of oxygen-isotope profiles from modern *P.*  
402 *magellanicus* provided by Chute et al. (2012) suggests that they constitute summer  
403 records from individuals whose growth rate had declined, perhaps to zero for some  
404 intervals. The higher extreme values (i.e., lower peaks) than those in summer records  
405 from early ontogeny are an expected result of this (through time-averaging in  
406 sampling), as are the lower extreme values (i.e., shallower troughs) of intervening  
407 winter records in comparison with early ontogeny. Such ontogenetic reduction in the  
408 amplitude of seasonal oxygen-isotope cycles has been widely recognised in bivalves  
409 and makes it wise to concentrate on the first few years of growth in any attempt to  
410 document the full range of seasonal temperature fluctuation. For this reason, only  
411 information from the first and second winters and summers is incorporated in  
412 subsequent analysis.

413 Assignment of portions of the curves to summers or winters is generally  
414 uncontroversial but in certain cases either lateral truncation of the profile or ‘noise’  
415 makes it impossible to determine the relevant seasonal extreme with accuracy, and in  
416 a few instances ‘noise’ is sufficient to raise doubts about the seasonal assignment.  
417 Thus, truncation at the ventral margin makes it impossible to say whether the lowest  
418 values recorded for Summer 2 in VA1 and VA2 (Fig. 4A, 4C, respectively) are  
419 representative of the extreme conditions in the summers concerned. Similarly,  
420 truncation at the dorsal end of the profile makes it impossible to say whether the  
421 highest value recorded for Winter 1 in NC3 (Fig. 4G) is representative of the extreme  
422 conditions in the winter concerned. With respect to ‘noise’, while the portion of the  
423 profile from NC2 (Fig. 4F) corresponding to Winter 1 is clear, identification of the  
424 exact position and value for the winter extreme is made problematic by high-  
425 frequency variability; it could indeed be argued that the two-point increase in  $\delta^{18}\text{O}$

426 defining Summer 1 at the dorsal end of this profile together with the one-point  
427 decrease in  $\delta^{18}\text{O}$  defining Winter 1 at the dorsal end of the profile from VA4 (Fig. 4D)  
428 are both representative of ‘noise’. However, in at least the latter case the value for the  
429 winter extreme identified is similar to that of another winter extreme from the same  
430 shell. Uncertainties over seasonal recognition and the most appropriate value for  
431 seasonal extremes could be addressed by applying a smoothing function (e.g., Wang  
432 et al., 2015) but this would lead to an underestimation of seasonal range in cases  
433 where the extreme values measured are probably not representative of the extreme  
434 conditions experienced by the animal – i.e., where an extreme value derives from a  
435 sample close to a growth-break (blue triangles in Fig. 4). Such cases are not  
436 uncommon: the Summer 1 extremes in VA1, VA3, NC1 and NC4, the Summer 2  
437 extremes in VA2, VA3, NC1 and NC3, and the Winter 2 extremes in VA3 and NC3  
438 are from samples taken 0.5-1.5 mm from a major or moderate growth break, and there  
439 are other cases where seasonal extremes are from samples a little farther from growth  
440 breaks. Under these circumstances it seems best not to apply a smoothing function but  
441 to take the most extreme value measured for a given season as representative of the  
442 extreme conditions experienced. This has the additional benefit of enabling like-with-  
443 like comparison with data from previous isotopic studies of Yorktown Formation  
444 bivalves (Krantz, 1990; Goewert and Surge, 2008; Winkelstern et al., 2013). While  
445 the most extreme conditions experienced by the organism in a given winter or  
446 summer are probably not recorded in cases where the relevant measured extreme  
447 derives from a sample close to a growth break, it is unlikely that the measured value is  
448 seriously unrepresentative in years 1 and 2 because ‘spring’ and ‘fall’ growth breaks  
449 at this age (e.g., Fig. 4A-C, 4G) are rarely associated with any steepening of the  $\delta^{18}\text{O}$   
450 profile, implying that growth interruptions were generally brief.

451 Table 2 shows the extreme  $\delta^{18}\text{O}$  values for the winter and summer periods  
452 identified. The 13 winter values range from +1.80‰ to +2.73‰. Of the six lowest  
453 values, four (+1.90‰, +1.91‰, +2.01‰, +2.15‰) are second values from shells  
454 showing another winter value of +2.25‰ or more. Of these four, one (Winter 1: NC3)  
455 is from the dorsal end of a profile and may well reflect truncation, while the other  
456 three (Winter 2: VA3, NC1, NC2) might be early manifestations of ontogenetic  
457 reduction in growth-rate (combined with temporary cessation of growth in VA3),  
458 leading to greater time-averaging in sampling. The mean of all the winter values  
459 ( $+2.24 \pm 0.3\%$ ;  $\pm 1\sigma$ ) may therefore be a less accurate guide to typical extreme winter  
460 temperature on the seafloor than the mean of the highest winter value from each shell  
461 ( $+2.42 \pm 0.23\%$ ). The highest winter values of the coarsely sampled shells are all less  
462 than those of the finely sampled shells, and the lowest and third lowest winter values  
463 recorded (+1.80‰ and +2.00‰) are from the most coarsely sampled shell (VA4),  
464 suggesting that higher values went undetected in coarse sampling. Notwithstanding  
465 the small sample size (4), the mean of the highest winter value from the finely  
466 sampled shells ( $+2.61 \pm 0.10\%$ ) is therefore probably the very best guide to typical  
467 extreme winter temperature on the sea floor. Whether comparing all the winter values  
468 from the Virginia and North Carolina shells (means:  $+2.29 \pm 0.34\%$ ,  $+2.20 \pm 0.25\%$ ,  
469 respectively), the highest winter values (means:  $+2.44 \pm 0.30\%$ ,  $+2.40 \pm 0.12\%$ ,  
470 respectively) or the highest winter values from finely sampled shells (means:  $+2.71 \pm$   
471  $0.02\%$ ,  $+2.51 \pm 0.04\%$ ), the means from the North Carolina shells are consistently a  
472 fraction lower, suggesting a corresponding slight difference in winter benthic  
473 temperature.

474 The 14 summer values for  $\delta^{18}\text{O}$  in Table 2 range from +0.98‰ to  $\square$ 0.13‰. The  
475 highest value (Summer 1: NC2) may well be representative of ‘noise’ rather than

476 summer conditions. The high Summer 2 values from VA3 (+0.62‰) and NC2  
477 (+0.67‰) are from samples respectively on or quite close (3.3 mm) to a growth break  
478 (Fig. 4C, 4F) and therefore may not give an accurate picture of the extreme summer  
479 conditions experienced. The same could apply to the high Summer 1 value (+0.69‰)  
480 from NC4, from a sample close (1.5 mm) to a growth break (Fig. 4H), and to those  
481 lower summer values which are from samples close or quite close to growth breaks  
482 (Summer 1: VA1, VA3, NC1; Summer 2: VA2, NC1, NC3) and/or at the end of  
483 laterally truncated profiles (Summer 2: VA1, VA2). However, while these values may  
484 not give a wholly accurate picture of extreme conditions in the summers concerned, it  
485 is unlikely that they are grossly misleading because they span a range (□0.13‰ to  
486 +0.69‰) which is similar to that spanned by values which are neither from samples  
487 close to growth breaks nor from the ends of truncated profiles (Summer 1: VA2, NC3;  
488 □0.03‰, +0.56‰, respectively). It is also unlikely that sampling strategy has  
489 influenced the results much because for North Carolina shells the mean of summer  
490 values from coarsely sampled shells ( $+0.52 \pm 0.15\text{‰}$ ) is only slightly higher than  
491 from finely sampled shells ( $+0.37 \pm 0.23\text{‰}$ ;  $+0.52 \pm 0.33\text{‰}$  if the questionable very  
492 high value from NC2 is included) and the same is true for Virginia shells (coarse:  
493  $+0.24 \pm 0.31\text{‰}$ ; fine:  $+0.17 \pm 0.23\text{‰}$ ). The mean of all summer values is  $+0.31 \pm$   
494  $0.27\text{‰}$  ( $+0.36 \pm 0.31\text{‰}$  if the questionable value from NC2 is included), and the mean  
495 of North Carolina values ( $+0.45 \pm 0.21\text{‰}$ ;  $+0.52 \pm 0.27\text{‰}$  if the questionable value  
496 from NC2 is included) is somewhat higher than the mean of Virginia values ( $+0.20 \pm$   
497  $0.27\text{‰}$ ), suggesting a corresponding small difference in summer seafloor temperature.  
498

499 *Carbon Isotopes.*—Most  $\delta^{13}\text{C}$  values (Fig. 4) are positive but, with the exception  
500 of VA4 (Fig. 4D), all the profiles show more or less pronounced ontogenetic trends to

501 lower values such that those from late ontogeny are often negative. Superimposed on  
502 the ontogenetic reduction, and displayed in every profile, is a cyclicity in  $\delta^{13}\text{C}$  which  
503 parallels that in  $\delta^{18}\text{O}$  except in the early ontogeny of VA1, VA2, VA4 and NC3 (Fig.  
504 4A, 4B, 4D, 4G, respectively), where there are slight offsets or additional oscillations.  
505 The range of mean  $\delta^{13}\text{C}$  values from North Carolina shells (NC1:  $+0.44 \pm 0.66\text{‰}$ ,  
506 NC2:  $+0.77 \pm 0.54\text{‰}$ , NC3:  $+0.08 \pm 0.49\text{‰}$ , NC4:  $+0.65 \pm 0.58\text{‰}$ ) is less than from  
507 Virginia shells (VA1:  $+1.01 \pm 0.56\text{‰}$ , VA2:  $+1.09 \pm 0.50\text{‰}$ , VA3:  $-0.04 \pm 0.44\text{‰}$ ,  
508 VA4:  $+0.50 \pm 0.29\text{‰}$ ) and the mean of the mean values from North Carolina shells  
509 ( $+0.49 \pm 0.26\text{‰}$ ) is also less than from Virginia shells ( $+0.64 \pm 0.45\text{‰}$ ).

510

511 *Microgrowth Increments.*—Trendlines (five-point averages) are included with the  
512 raw increment data in Figure 4. These show low amplitude, high frequency variation,  
513 particularly in the North Carolina shells, but in the Virginia shells VA1 and VA2 (Fig.  
514 4A, 4C, respectively) a rather higher amplitude, lower frequency oscillation of about  
515 six cycles per annum is evident. Superimposed on this in VA2, also discernible in  
516 VA3 (Fig. 4C), and of high amplitude in VA4 (Fig. 4D) is an approximately annual  
517 cycle of increment size variation, which is also evident in the North Carolina shells  
518 NC1, NC3 and NC4 (Fig. 4E, 4G, 4H, respectively), and of high amplitude in NC3.  
519 The cycles are typically offset somewhat from those of  $\delta^{18}\text{O}$  variation. NC2 (Fig. 4F)  
520 shows a supra-annual overall pattern of increment size variation.

521

522

## Discussion

523

524 *Shell Preservation.*—While the anomalous  $\delta^{18}\text{O}$  values discussed above are only  
525 explicable by diagenesis in the case of one shell, it might be argued that the

526 covariation between  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  noted in every shell is evidence of pervasive  
527 alteration through interaction with meteoric waters, since these typically have low  
528  $\delta^{18}\text{O}$  and low  $\delta^{13}\text{C}$  signatures. However, the wavelengths of  $\delta^{18}\text{O}$  cycles from *P.*  
529 *clintonius* (typically 40-50 mm between Summer/Winter 1 and 2, decreasing  
530 thereafter; Fig. 4) are like those derived from modern *P. magellanicus* at a similar  
531 stage in ontogeny, and which undoubtedly relate to seasonal changes in ambient  
532 temperature (Krantz et al., 1984; Chute et al., 2012). The covariance of  $\delta^{13}\text{C}$  with  
533  $\delta^{18}\text{O}$  must therefore relate to environmental changes which follow the seasonal  
534 temperature cycle rather than to diagenesis. Parallelism between  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$   
535 profiles has been noted in modern *P. magellanicus*, as has ontogenetic reduction in  
536  $\delta^{13}\text{C}$  like that seen in *P. clintonius* (Krantz et al., 1987, 1988), so there can be little  
537 doubt that the isotopic composition of samples from the latter is essentially original.  
538

539 *Paleohydrography.*— $\delta^{18}\text{O}$  from bivalves provides a record of temperature in the  
540 benthic environment, but an estimate of SST is required for purposes of comparison  
541 with numerical models. In the shallow shelf (0-20 m), winter benthic temperature is  
542 usually almost identical to SST, and summer surface and seafloor temperatures are  
543 typically also about the same. In the mid-shelf (20-40 m), winter benthic temperature  
544 is usually only a little different from SST (typically a degree or two higher; e.g.,  
545 Winkelstern et al., 2013) but, as indicated above, summer benthic temperature can be  
546 substantially lower than SST as a result of incomplete mixing down of warm, low  
547 density surface waters. The amount of difference is dependent on the intensity of  
548 summer heating, the depth of water and the degree of agitation by wave and current  
549 action.

550 Attempts have been made to characterise hydrographic setting in terms of the  $\delta^{13}\text{C}$   
551 of bivalves. Arthur et al. (1983) documented an antiphase relationship between  $\delta^{13}\text{C}$   
552 and  $\delta^{18}\text{O}$  in a modern specimen of *Spisula solidissima* from 10 m depth and an in-  
553 phase pattern in two further specimens from 45 m depth, below the summer  
554 thermocline. They considered that this difference reflected removal of  $^{12}\text{C}$  from  
555 surface waters by photosynthesis during the summer (giving high  $\delta^{13}\text{C}$  alongside low  
556  $\delta^{18}\text{O}$  in the 10 m specimen) and supply of  $^{12}\text{C}$  to deep benthic waters during the  
557 summer by oxidation of sedimented organic matter (giving low  $\delta^{13}\text{C}$  alongside low  
558  $\delta^{18}\text{O}$  in the 45 m specimens). The in-phase pattern occurs in modern *Placopecten*  
559 *magellanicus* from 57 m (Krantz et al., 1987, 1988) so on the basis of its pervasive  
560 occurrence in the analysed *P. clintonius* one might infer a similar sub-thermocline  
561 setting for these shells. However, an antiphase pattern was recorded by Johnson et al.  
562 (2009, fig. 5) in a modern *Aequipecten opercularis* specimen from a sub-thermocline  
563 setting at 50 m (Gulf of Tunis, Mediterranean Sea), and in-phase  $\delta^{13}\text{C}/\delta^{18}\text{O}$  variation  
564 was recorded by Krantz et al. (1987, figs. 4, 5) in modern *S. solidissima* from 14 m, a  
565 depth almost certainly above the summer thermocline. Possible explanations exist for  
566 these exceptions (e.g., in summer, insufficient dissolved oxygen and insufficient  
567 nutrients, respectively); however, the important point is that patterns of  $\delta^{13}\text{C}$  variation  
568 in relation to  $\delta^{18}\text{O}$  are not an infallible guide to hydrographic setting.

569 Independent evidence may be supplied by patterns of microgrowth increment size,  
570 especially in early ontogeny. The modern sub-thermocline specimen of *A. opercularis*  
571 referred to above was only one year old at death from the evidence of its  $\delta^{18}\text{O}$  profile  
572 (Fig. 5B, red line). It shows some fairly low amplitude, high frequency fluctuation in  
573 increment size but superimposed on this is a high amplitude, approximately annual  
574 cycle of variation, out of phase with that of  $\delta^{18}\text{O}$  (Fig. 5A, blue line). Similar

575 increment patterns occur in other specimens from the same location (Fig. 5A, green  
576 and yellow lines), but their relationship with  $\delta^{18}\text{O}$  is not known. However, high  
577 amplitude, annual-scale variation, out of phase with  $\delta^{18}\text{O}$  in early ontogeny (to an age  
578 of about 1.5 years) but in phase later, occurs widely in fossil specimens of *A.*  
579 *opercularis* from the inferred stratified setting of the Pliocene Coralline Crag in  
580 eastern England (Johnson et al., 2009). By contrast, sub-fossil examples from the  
581 fairly shallow (mostly <40 m), strongly tidal and hence continuously well-mixed  
582 waters of the southern North Sea show no annual cycle or only a low amplitude one,  
583 usually in phase with  $\delta^{18}\text{O}$  in early ontogeny (Fig. 5B). The majority of the  
584 investigated specimens of *P. clintonius* show an annual-scale variation in increment  
585 size. This is of high amplitude and out of phase with  $\delta^{18}\text{O}$  in some from both Virginia  
586 and North Carolina (markedly so in the early ontogeny of VA2 and NC3; Fig. 4B, 4G,  
587 respectively). Thus, by analogy with increment patterns in *A. opercularis*, it can be  
588 deduced that seasonal stratification occurred in both areas. Microgrowth increment  
589 evidence therefore supports the argument based on the pattern of  $\delta^{13}\text{C}$  variation in  
590 relation to  $\delta^{18}\text{O}$ . The inference of seasonal stratification is consistent with the 20-40 m  
591 depth estimate of Ward et al. (1991), since within this range on the modern shelf  
592 adjacent to the studied areas water temperature is notably cooler than at the surface in  
593 summer (see above).

594

595 *Seafloor and Surface Paleotemperatures.*—Isotope-derived temperatures are  
596 dependent on the value selected for  $\delta^{18}\text{O}_{\text{seawater}}$  (Equation 1). Previous work on  
597 Pliocene scallops of the Middle Atlantic Coastal Plain (Krantz, 1990; Goewert and  
598 Surge, 2008) used a variety of mainly somewhat negative values based on the fact that  
599 global ice volume was generally lower than now. Modelling of regional variation,

600 taking account of differences in evaporation and precipitation, yields positive  
601  $\delta^{18}\text{O}_{\text{seawater}}$  for the area in question: +0.7‰ for the early Pliocene and +1.1‰ for the  
602 mid-Pliocene (Williams et al., 2009). Our preferred estimates of temperature for the  
603 early Pliocene Sunken Meadow Member are based on calculations using the former  
604 value. However, we also supply the results of calculations using the latter value and,  
605 for reference, the most extreme negative value used in earlier work on material from  
606 the Sunken Meadow Member ( $\square$ 0.4‰; Krantz, 1990). Figure 6 shows profiles of  
607 isotope-derived temperature from each shell using the three values of  $\delta^{18}\text{O}_{\text{seawater}}$ , with  
608 the preferred data shown by a thicker line. Summer and winter extreme values are  
609 listed in Table 2. While salinity, and hence  $\delta^{18}\text{O}_{\text{seawater}}$ , might not have been constant  
610 through the year, any significant departures from normal would probably have been in  
611 the spring (from freshwater run-off; see above), so the calculated summer and winter  
612 extreme temperatures do not need any adjustment for short-term salinity variation.

613 Using the preferred value for  $\delta^{18}\text{O}_{\text{seawater}}$  (+0.7‰), all the shells except VA4 (the  
614 most coarsely sampled) yield at least one winter minimum temperature below the  
615 lower limit for a warm temperate marine climate (10 °C), and the finely sampled  
616 shells all yield such a temperature even using the more positive value for  $\delta^{18}\text{O}_{\text{seawater}}$   
617 (+1.1‰). Using the preferred value for  $\delta^{18}\text{O}_{\text{seawater}}$ , VA3 shows a second winter  
618 minimum temperature below 10 °C but second minima from other shells (NC1, NC2,  
619 NC3) are slightly above 10 °C. For NC3 (Winter 1) truncation of the profile is a likely  
620 explanation but for NC1 and NC2 (both Winter 2) neither this, nor the existence of  
621 growth breaks, can be invoked. While a general slowing of growth may have been  
622 contributory in the case of NC1 and NC2, it seems more reasonable to conclude that  
623 the evidence from these shells of slightly warmer winters in some years reflects a  
624 slightly higher mean benthic winter temperature in North Carolina than Virginia.

625 Nevertheless, the temperature ( $9.3 \pm 0.9$  °C;  $\pm 1\sigma$ ) calculated from the mean of all  
626 winter (extreme)  $\delta^{18}\text{O}$  values from North Carolina shells using the preferred value for  
627  $\delta^{18}\text{O}_{\text{seawater}}$  is, like the corresponding temperature calculated from Virginia values ( $9.0$   
628  $\pm 1.3$  °C), still below the lower limit for a warm temperate marine climate. As argued  
629 above, the most accurate indication of typical extreme winter temperature on the  
630 seafloor may be supplied by the mean of the highest winter  $\delta^{18}\text{O}$  value from each of  
631 the finely sampled shells. The temperatures so-derived for North Carolina ( $8.2 \pm 0.2$   
632 °C) and Virginia ( $7.4 \pm 0.1$  °C) are even farther below the lower limit for a warm  
633 temperate marine climate. Given the estimated depth of the shells and the likelihood  
634 of a small insulating effect from the overlying water, winter surface temperature was  
635 probably a degree or two lower than seafloor temperature and thus very firmly within  
636 the mild/cool temperate range over the whole of the studied area.

637 Using the preferred value for  $\delta^{18}\text{O}_{\text{seawater}}$  ( $+0.7\text{‰}$ ), all 14 values for summer  
638 seafloor temperature are below the lower limit ( $22.5$  °C) of a warm temperate marine  
639 climate yet within the range (upper boundary:  $21\text{--}23.5$  °C; Dickie, 1958) tolerated by  
640 modern *P. magellanicus*. The lowest value (Summer 1 of NC2) may be an artefact of  
641 noise and a significant underestimate of the maximum temperature experienced. Some  
642 other values are probably also underestimates of benthic temperature due to the  
643 effects of growth breaks, coarse sampling and truncation of the data series, but are  
644 unlikely to be seriously misrepresentative. The temperatures calculated from the mean  
645 of all summer  $\delta^{18}\text{O}$  values from Virginia shells, North Carolina shells and the two sets  
646 combined (excluding Summer 1 of NC2 in the last two cases) are, respectively,  $17.5 \pm$   
647  $1.2$  °C,  $16.4 \pm 0.9$  °C and  $17.0 \pm 1.2$  °C. While these figures are probably fairly  
648 accurate for the seafloor, they are likely to be significant underestimates of SST, by an  
649 amount in the order of  $6$  °C on the basis of the likely temperature/depth profile in

650 summer. Adding this amount to all the individual summer values (excluding Summer  
651 1 in NC2) yields temperatures above the lower limit for a warm temperate marine  
652 climate for five of the seven Virginia estimates and for three of the six North Carolina  
653 estimates. Adding 6 °C to the temperature calculated from the mean of all summer  
654  $\delta^{18}\text{O}$  values for each of Virginia and North Carolina (excluding Summer 1 in NC2)  
655 yields for the former a temperature above (23.5 °C) and for the latter a temperature  
656 fractionally below (22.4 °C) the warm temperate range. It is implausible that summer  
657 SST was actually lower in North Carolina than Virginia (farther north) so it may be  
658 that the shells from the former area occupied slightly deeper water and that a larger  
659 ‘stratification factor’ should have been applied.

660 While there is a solid basis for favouring those temperature estimates for the  
661 Sunken Meadow Member based on a value for  $\delta^{18}\text{O}_{\text{seawater}}$  of +0.7‰, it cannot be  
662 denied that some uncertainty attaches to the absolute values obtained. Very little  
663 uncertainty attaches to estimates of seasonal range (i.e., relative temperature) because  
664 this parameter is only slightly affected by the value adopted for  $\delta^{18}\text{O}_{\text{seawater}}$  (e.g., only  
665 a 1.2 °C difference between the range estimates using  $\delta^{18}\text{O}_{\text{seawater}} = \square 0.4\text{‰}$  and  
666 +1.1‰ for the largest range in  $\delta^{18}\text{O}_{\text{calcite}}$  observed, in VA1). Using a  $\delta^{18}\text{O}_{\text{seawater}}$  value  
667 of +0.7‰ and calculating mean benthic seasonal range from the temperatures  
668 specified by the means of the most extreme winter and summer  $\delta^{18}\text{O}$  values from each  
669 shell (for winter:  $8.4 \pm 1.1$  °C in Virginia,  $8.6 \pm 0.4$  °C in North Carolina,  $8.5 \pm 0.9$  °C  
670 in both areas combined; for summer:  $18.2 \pm 0.6$  °C in Virginia,  $16.5 \pm 1.1$  °C in North  
671 Carolina,  $17.3 \pm 1.2$  °C in both areas combined) yields figures of 9.8 °C for Virginia,  
672 7.9 °C for North Carolina and 8.8 °C for both areas combined. These figures, which  
673 can be regarded as maximum estimates, are not very different from those (8.5 °C, 7.1  
674 °C, 7.8 °C, respectively) calculated from the means of all winter and summer  $\delta^{18}\text{O}$

675 values (excluding Summer 1 in NC2) from the Virginia, North Carolina and  
676 combined shells, which can be regarded as minimum estimates. From the fact that in  
677 the present-day MAB, shelf surface temperature is higher than at 30 m by about 6 °C  
678 in summer and lower than at 30 m by about 2 °C in winter (Winkelstern et al., 2013),  
679 it can be reasonably surmised that the seasonal range in SST when the analysed *P.*  
680 *clintonius* specimens were alive was about 8 °C more than the benthic estimates  
681 derived from them, i.e., about 17 °C in Virginia and 15.5 °C in North Carolina.

682 The figures for absolute summer and winter seafloor temperatures derived above  
683 are very similar to those obtained by Krantz (1990) through an isotopic study of the  
684 scallop *Chesapecten jeffersonius* from the upper Sunken Meadow Member. However,  
685 the temperatures from *C. jeffersonius* become significantly higher than those from *P.*  
686 *clintonius* when calculated using the preferred value for  $\delta^{18}\text{O}_{\text{seawater}}$  (see below). The  
687 estimate for summer temperature obtained by Hazel (1971, 1988) from analysis of  
688 Sunken Meadow ostracod assemblages is consistent with the benthic summer figures  
689 from *P. clintonius*, but his estimate for winter temperature (at least 12.5 °C) is  
690 markedly higher than the winter estimate from *P. clintonius*. Possibly ostracod  
691 assemblage composition is controlled more by summer temperature than winter and  
692 gives inaccurate indications of the latter.

693

694 *Paleoclimate and Paleoceanography.*—The estimates derived above for absolute  
695 surface temperature in summer and winter, and for surface seasonal range, are very  
696 comparable with present-day figures for offshore locations in the MAB but differ in  
697 all respects from present-day figures for offshore locations in the SAB, including a  
698 location immediately south of the latitude of Cape Hatteras (Table 1). The data  
699 derived from *P. clintonius* in Virginia thus show that surface conditions there when

700 the animals were alive closely resembled those on the adjacent shelf now, but the data  
701 derived from *P. clintonius* in North Carolina (from a location at the same latitude as  
702 Cape Hatteras) reveal that much the same conditions also existed some 210 km farther  
703 south, where now shelf surface temperatures are higher, particularly in winter.

704 It is possible to invent explanations involving multiple causes for the  
705 circumstances indicated by the *P. clintonius* data. For instance, one could propose a  
706 cooler general climate combined with warm-current flow farther north, the former  
707 outweighing current influence in North Carolina and balancing it in Virginia.  
708 However, an explanation involving a single cause – cool-current flow farther south  
709 (Cronin and Dowsett, 1996) – is available and should be favoured on grounds of  
710 parsimony alone. In fact there are additional grounds for favouring this explanation.  
711 Firstly, despite the barrier created by Cape Hatteras at present, northern shelf waters  
712 probably penetrate into the SAB more than 50% of the time through wind-forcing  
713 (Pietrafesa et al., 1994). Secondly, the cool surface waters of the Slope Sea adjacent to  
714 the shelf north of Cape Hatteras have a higher nutrient content and primary  
715 productivity than the warm Gulf Stream farther offshore (Fig. 7); flow of these waters  
716 farther south to replace the Gulf Stream at the shelf edge (i.e., extension of the ‘slope  
717 current’; Fig. 8), with intrusions onto the shelf as occur from the Gulf Stream now,  
718 provides a plausible explanation for the diverse fish fauna of the Sunken Meadow  
719 Member in North Carolina (Fierstine, 2001; Purdy et al., 2001) and the similarly  
720 diverse bird fauna, including many seabirds dependent on a rich marine food source  
721 (Olson and Rasmussen, 2001). Phosphate once thought to be primary and related to  
722 high productivity is now considered to be reworked from Miocene deposits (Riggs et  
723 al., 2000). However, the benthic foraminifera of the Sunken Meadow in North  
724 Carolina are still consistent with high nutrient supply (Snyder et al., 2001). The

725 present-day shelf of southeastern South America from 38-32 °S (i.e., to a latitude  
726 lower than that of Cape Hatteras) provides an illustration of the scenario envisaged.  
727 Here, very high primary productivity (>500 mgC/m<sup>2</sup>/day and locally 770  
728 mgC/m<sup>2</sup>/day) supports major secondary production, including large populations of  
729 commercially exploited fish (Bisbal, 1995). Discharge of terrestrially derived  
730 nutrients from the Rio de La Plata and Patos-Mirim Lagoon system undoubtedly  
731 contributes to the productivity. However, it is also supported by supply of nutrients  
732 from the cold equatorward-flowing waters of the Falklands/Malvinas Current. These  
733 waters are at the 150-200 m isobath north of 35 °S (equivalent to the latitude of Cape  
734 Hatteras) but are locally returned to the surface on the shelf as far north as 23 °S  
735 through offshore Ekman transport caused by winds blowing south-west (alongshore)  
736 on the western side of the South Atlantic subtropical anticyclone. Given similar  
737 equatorward penetration of cold ‘surface’ waters on the western side of the North  
738 Atlantic during the Pliocene in the absence of a feature analogous to Cape Hatteras,  
739 winds blowing north-east on the western side of the subtropical anticyclone would  
740 likewise have led to nutrient enrichment of shelf waters. Greater southward spread of  
741 northern surface waters provides an explanation for the grand mean  $\delta^{13}\text{C}$  values from  
742 *P. clintonius* in North Carolina and Virginia which, although different and lower for  
743 the southern area, are evidently much less so than the  $\delta^{13}\text{C}$  values from modern outer  
744 shelf specimens of *Argopecten gibbus* in the SAB compared to outer shelf specimens  
745 of *P. clintonius* in the MAB (Krantz et al., 1988).

746 Reversal of the current pattern proposed above – i.e., extension of warm-current  
747 influence into the area of Virginia – is a simple and attractive explanation for the mid-  
748 Pliocene warming evinced by the higher members of the Yorktown Formation, and, as  
749 noted above, has been widely adopted. However, it is theoretically possible that cold-

750 current flow continued over the area of deposition but its effect on water temperature  
751 was outweighed by general climatic warming. We evaluate this possibility in the next  
752 section through an investigation of isotopic temperatures from the upper part of the  
753 Sunken Meadow Member and from the higher members of the Yorktown Formation.  
754 We take particular note of the evidence of seasonal temperature range, since this is  
755 almost independent of the value used for  $\delta^{18}\text{O}_{\text{seawater}}$  and is a parameter which can  
756 determine whether warming was caused by northward extension of warm-current  
757 influence. This circumstance would effectively bring the conditions of the modern  
758 SAB into the area of Virginia. Maps of average monthly benthic temperature supplied  
759 by Atkinson et al. (1983) enable reconstruction of the present benthic seasonal range  
760 over the SAB. Oceanward of the mid-shelf, the range is less than 10 °C, and landward  
761 it is more. However, only in very nearshore locations, in water shallower than 20 m, is  
762 the benthic seasonal range above 15 °C. Hence, any significant evidence of a benthic  
763 seasonal range greater than 15 °C from the higher Yorktown Formation would argue  
764 against northward extension of warm-current influence.

765

766 ISOTOPIC TEMPERATURES FROM  
767 THE HIGHER YORKTOWN FORMATION

768

769 Data from Other Scallop Genera

770

771 *Placopecten* does not occur in the Yorktown Formation above the basal section of  
772 the Sunken Meadow Member. However, the extinct scallop genera *Chesapecten* and  
773 *Carolinapecten* occur in all four members. They do not occur with brackish-water  
774 taxa and it can therefore be assumed that they were stenohaline marine, tolerating

775 only brief reductions in salinity. Krantz (1990) obtained profiles of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$   
776 from *Chesapecten jeffersonius* of the upper part of the Sunken Meadow Member, *C.*  
777 *madisonius* of the Rushmere and Moore House members and *Carolinapecten eboreus*  
778 of the Morgarts Beach and Moore House members. Further profiles from *C.*  
779 *madisonius* of the Moore House Member were obtained by Goewert and Surge  
780 (2008). These authors listed the extreme  $\delta^{18}\text{O}$  values from each specimen. We have  
781 used their data, in conjunction with appropriate figures for  $\delta^{18}\text{O}_{\text{seawater}}$ , to calculate  
782 maximum estimates of benthic seasonal temperature range for comparison with the  
783 test value identified above. We have employed the equation (1) and set of  $\delta^{18}\text{O}_{\text{seawater}}$   
784 values ( $\square 0.4\text{‰}$ ,  $+0.7\text{‰}$ ,  $+1.1\text{‰}$ ) used for *Placopecten clintonius* to derive figures for  
785 winter and summer benthic temperature for each specimen (Table 2), although  
786 arguably for the mid-Pliocene material the low value for  $\delta^{18}\text{O}_{\text{seawater}}$  should have been  
787 set at  $-0.6\text{‰}$  for Rushmere and Morgarts Beach individuals and  $-0.5\text{‰}$  for Moore  
788 House individuals in recognition of the use of these figures by Krantz (1990) and  
789 Goewert and Surge (2008). Following Williams et al. (2009), our preferred value for  
790 these units is  $+1.1\text{‰}$ . Although our focus is the seasonal range in benthic temperature,  
791 we comment below on the winter and summer benthic temperatures from which the  
792 ranges are derived, and also attempt to determine surface temperatures using the  
793 evidence of depth supplied by patterns of variation in  $\delta^{13}\text{C}$  relative to  $\delta^{18}\text{O}$ , together  
794 with other indicators. The sampling of *Chesapecten* and *Carolinapecten* shells by  
795 Krantz (1990) and Goewert and Surge (2008) was in the outer shell layer but at a  
796 higher spatial resolution (1 mm or less) than our sampling of *Placopecten* shells;  
797 hence, although few in number for some horizons, the estimates of seasonal benthic  
798 (and surface) temperature for the higher Yorktown Formation are certainly at least as  
799 reliable as those for the basal part of the Sunken Meadow Member.

800

801 *Upper Sunken Meadow Member.*—Krantz (1990) obtained isotope profiles from  
802 three specimens of *Chesapecten jeffersonius* from two locations on the James River,  
803 Virginia, close to the collection locations of the specimens of *Placopecten clintonius*  
804 from Virginia discussed above. The two specimens (SM-CJ1, SM-CJ2) from the first  
805 location, Sunken Meadow Creek (the Sunken Meadow type locality; 4 in Fig. 2B),  
806 were collected about 1 m above the base of the member and the single specimen  
807 (KING-CJ) from the second, Kingsmill (5 in Fig. 2B), immediately below the contact  
808 with the overlying Rushmere Member, 2-3 m above the base of the Sunken Meadow  
809 Member (Ward and Blackwelder, 1980, fig. 22). The interpretation of depth and  
810 water-column structure derived for the basal Sunken Meadow Member from the  
811 pattern of variation in  $\delta^{13}\text{C}$  in relation to  $\delta^{18}\text{O}$  within *P. clintonius* shells can also be  
812 applied to higher horizons from the evidence of strong parallelism in the profiles  
813 derived from *C. jeffersonius* specimens KING-CJ and SM-CJ1 by Krantz (1990, figs.  
814 3b, c). Krantz ascribed the lack of parallelism in SM-CJ2 (1990, fig. 3a) to diagenesis.  
815 All three specimens contain at least one winter record of  $\delta^{18}\text{O}$ . The temperatures  
816 derived from the most extreme values represented in each shell for the preferred value  
817 of  $\delta^{18}\text{O}_{\text{seawater}}$  (+0.7‰; Table 2) give a winter mean of  $11.4 \pm 0.7$  °C ( $\pm 1\sigma$ ). The  
818 equivalent for summer (based on only two extreme values because SM-CJ1 lacks a  
819 full summer record) is  $23.0 \pm 1.0$  °C. The winter mean may be a slight overestimate  
820 and the summer mean a slight underestimate because the winter value from SM-CJ2  
821 and the summer value from KING-CJ are each from samples close to major growth  
822 breaks. Because these potential errors have opposite effects on the estimate of annual  
823 range, the figure (11.6 °C) derived for this from the winter and summer means is  
824 probably quite accurate. The figures for winter and summer mean temperature,

825 median temperature (17.2 °C; taken as an approximation of annual mean temperature)  
826 and for annual range are all notably higher than the corresponding figures for *P.*  
827 *clintonius* in Virginia (respectively, 8.4 °C, 18.2 °C, 13.3 °C, 9.8 °C), and also North  
828 Carolina (8.6 °C, 16.5 °C, 12.6 °C, 7.9 °C). While the higher summer temperature and  
829 annual range might reflect closer sample spacing, this would not have led to  
830 recognition of a higher winter temperature. Thus, although one must acknowledge the  
831 rather small sample size, the data from *C. jeffersonius* in the upper part of the Sunken  
832 Meadow Member does seem to suggest warmer conditions on the seafloor. It also  
833 suggests warmer surface temperatures: about 9.5 °C in winter and 29 °C in summer  
834 from the arguments applied to *P. clintonius*, giving a median temperature (19.3 °C)  
835 which is higher than is specified by modern winter and summer surface temperatures  
836 at any location in the MAB (Table 1). While the increase in benthic seasonal range  
837 from that indicated by the earlier *P. clintonius* shells is not sufficient to meet the test  
838 criterion of a value of 15 °C, it is consistent with the idea that higher seawater  
839 temperatures were brought about by a warming of general climate rather than  
840 increased influence of warm currents from the south.

841

842 *Rushmere and Morgarts Beach Members.*—It is unfortunate that published isotope  
843 profiles exist for only single scallop specimens from each of these members, which  
844 were deposited as the result of a major transgression, leading to the highest stand of  
845 sea level in the late Neogene (Krantz, 1991) and the establishment of marine  
846 conditions across the Atlantic Coastal Plain from Maryland to Florida. Figure 2B  
847 shows the coastline according to Ward et al. (1991, fig. 16-4B), which is similar to the  
848 reconstruction of Rowley et al. (2013). Its only slightly curvilinear form would have  
849 presented no obstruction to northward- or southward-flowing currents, but shoals

850 identified by Ward et al. (1991) in the area of the Mid-Carolina Platform High would  
851 have restricted the passage of warm waters into northeast North Carolina and  
852 southeast Virginia. Winkelstern et al. (2013) placed the Morgarts Beach Member  
853 within the MPWP but considered that the lower part of the underlying Rushmere  
854 Member might have been deposited before it, a deduction consistent with the 4.0-3.0  
855 Ma age range for both members indicated by microfossil biostratigraphy (Krantz,  
856 1991; Fig. 1). Whatever the time of onset of the transgression, assemblage evidence  
857 from ostracods (Hazel, 1971, 1988; Cronin, 1991), mollusks (Ward et al., 1991) and  
858 foraminifers (Dowsett and Wiggs, 1992) points unequivocally to warmer ('warm  
859 temperate') conditions in southeast Virginia and northeast North Carolina during  
860 deposition of the Rushmere and Morgarts Beach members than during Sunken  
861 Meadow deposition.

862 Rushmere sediments are closely similar to those of the Sunken Meadow Member  
863 but sometimes with a larger admixture of clay (Ward and Blackwelder, 1980),  
864 suggesting quieter, somewhat deeper conditions, although still within the mid-shelf  
865 depth range (Krantz, 1991). The analysed specimen (BB-CM; Krantz, 1990, fig. 4a) is  
866 from near Fort Boykin, Burwell Bay, on the James River, Virginia (6 in Fig. 2B). The  
867  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  profiles show only short parallel trends and so provide no positive  
868 support for a seasonally stratified and hence fairly deep setting. Equally, however,  
869 they provide no clear support for a shallow setting. The winter and summer seafloor  
870 temperatures calculated from extreme  $\delta^{18}\text{O}$  values using the preferred (mid-Pliocene)  
871 value for  $\delta^{18}\text{O}_{\text{seawater}}$  (+1.1‰; Table 2) are, respectively, 13.3 °C and 29.3 °C (median:  
872 21.3 °C). These seasonal temperatures are considerably higher than the equivalents  
873 from any Sunken Meadow specimen (*P. clintonius* or *C. jeffersonius*) and entirely in  
874 accordance with previous deductions of very warm conditions during deposition of

875 the Rushmere Member. Even when calculated using a value for  $\delta^{18}\text{O}_{\text{seawater}}$  of +0.7‰,  
876 summer temperature (27.3 °C) is still higher than from all the Sunken Meadow  
877 specimens using the same value for  $\delta^{18}\text{O}_{\text{seawater}}$ ; however, winter temperature (11.7  
878 °C) is only higher than from the eight *P. clintonius* specimens and one (SM-CJ1) of  
879 the three *C. jeffersonius* specimens. Assuming the depth of the specimen was similar  
880 to that of Sunken Meadow specimens, and using the argument applied to them, yields  
881 for the Rushmere Member a surface winter temperature of about 11.5 °C and surface  
882 summer temperature of about 35.5 °C (this is not implausible given a modern record  
883 of 33 °C at a location 330 km north of Cape Hatteras; NDBC, undated, station  
884 OCIM2). The benthic seasonal range (16 °C, using +1.1‰ for  $\delta^{18}\text{O}_{\text{seawater}}$ ) supplied by  
885 the Rushmere Member specimen exceeds the 15 °C test criterion so, while one cannot  
886 draw firm conclusions from a single shell, the suggestion is of a warming of general  
887 climate rather than an increase in warm-current influence.

888 The analysed specimen of *Carolinapecten eboreus* from the Morgarts Berach  
889 Member (LTRUN-EB; Krantz, 1990, fig. 4b) is from Lieutenant Run, Petersburg,  
890 Virginia (7 in Fig. 2B). The setting is a barred embayment, probably quite shallow,  
891 notwithstanding the clayey silt sediment. The profile appears to record a winter  
892 minimum temperature – 12.5 °C using the preferred value for  $\delta^{18}\text{O}_{\text{seawater}}$  (+1.1‰) –  
893 which is again higher than any Sunken Meadow specimen (using  $\delta^{18}\text{O}_{\text{seawater}}$  =  
894 +0.7‰). Given the probable shallow setting, a similar surface temperature can be  
895 inferred. The profile lacks a full summer record but the highest temperature recorded  
896 (18.8 °C) indicates a median benthic temperature of at least 15.7 °C: higher than from  
897 the basal Sunken Meadow Member.  
898

899 *Moore House Member*.—This unit only occurs in a small area of southeast  
900 Virginia, with age-equivalent strata known locally in the subsurface of northeast  
901 North Carolina (Ward et al., 1991). It represents a further but less extensive  
902 transgression after a fall in sea level following the Rushmere/Morgarts Beach  
903 transgression. Figure 2B shows the coastline according to Ward et al. (1991, fig. 16-  
904 4C). The possible recurvature to the east indicated in the area of modern Cape  
905 Hatteras is a reflection of the absence of any unequivocally age-equivalent marine  
906 strata farther south (Krantz, 1991). While this may be a result of erosion (Ward and  
907 Blackwelder, 1980) it is quite possible that the Coastal Plain was emergent south of  
908 the area of Moore House occurrence, creating a barrier to the entry of warm waters. Sr  
909 isotope dating gives ages (2.6-2.5 Ma) well after the MPWP (Winkelstern et al., 2013)  
910 but microfossil biostratigraphy gives an older date (no younger than 2.8 Ma; Krantz,  
911 1990), and correlation with the eustatic sea level curve suggests an age of 3.1-3.0 Ma,  
912 i.e., within the MPWP (Krantz, 1991; Fig. 1). On the basis of the common presence of  
913 subtropical molluscan taxa at downdip (more easterly) locations, Ward et al. (1991)  
914 considered that the marine climate was even warmer than during the  
915 Rushmere/Morgarts Beach transgression. The three specimens of *Chesapecten*  
916 *madisonius* investigated by Goewert and Surge (2008) were collected from a  
917 sequence of glauconitic sands and shell hash at Riddick Pit, Chuckatuck, Virginia (8  
918 in Fig. 2B), about 50 km from the contemporary shoreline. The setting was probably  
919 an offshore bar, but one permanently submerged on the evidence of the fully marine  
920 associated fauna (including common *Glycymeris*, as well as *Marvacrassatella* and  
921 *Dinocardium*; A.L.A. Johnson, personal observations, 2007). While the sedimentary  
922 evidence suggests quite shallow, and hence well-mixed, waters, the strong covariation  
923 of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in two of the *C. madisonius* specimens (CMAD-4, CMAD-5;

924 Goewert and Surge, 2008, fig. 3b, 3c) seems to imply a deeper, seasonally stratified  
925 situation. It is possible, however, that the reductions in  $\delta^{13}\text{C}$  alongside the spring-  
926 summer reductions in  $\delta^{18}\text{O}$  in these specimens are an ontogenetic rather than  
927 environmental effect. The two specimens of *C. madisonius* and one of *Carolinapecten*  
928 *eboreus* investigated by Krantz (1990) were collected from a sequence of shelly sands  
929 at Yadkin Pit, near Deep Creek, Virginia (9 in Fig. 2B), some 25 km southeast of  
930 Chuckatuck and farther from the contemporary shoreline. The  $\delta^{13}\text{C}$  profiles of two  
931 specimens (YAD-EB1, YAD-CM1; Krantz, 1990, fig. 5b, 5c) are rather 'flat' and  
932 hence uninformative about hydrographic setting. That of the third (YAD-CM2;  
933 Krantz, 1990, fig. 5a) shows strong covariation of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ , which might reflect  
934 seasonal stratification but could, again, be an ontogenetic effect. The mean winter and  
935 summer seafloor temperatures calculated from all the extreme  $\delta^{18}\text{O}$  values using the  
936 preferred (mid-Pliocene) value for  $\delta^{18}\text{O}_{\text{seawater}}$  (+1.1‰; Table 2) are, respectively,  $12.0$   
937  $\pm 2.2$  °C and  $27.6 \pm 1.5$  °C, similar to the corresponding temperatures obtained from  
938 the single Rushmere and Morgarts Beach specimens, and the median temperature  
939 ( $19.8$  °C) is also similar to that from the Rushmere specimen. The winter mean is  
940 probably something of an overestimate because the raw values from all six specimens  
941 are from samples close to major growth breaks. The seasonal range calculated from  
942 the winter and summer means ( $15.6$  °C) is therefore likely to be somewhat  
943 underestimated. It is in any case higher than the test criterion, suggesting that the  
944 warm winter and summer benthic temperatures are the consequence of a warmer  
945 general climate rather than greater influence of warm currents. Given the conflicting  
946 evidence of depth from sedimentology and  $\delta^{13}\text{C}$  variation in relation to  $\delta^{18}\text{O}$ , seasonal  
947 surface temperatures are difficult to infer. However, it is important to point out that  
948 even if the water was shallow (<20 m) the interpretation of the benthic data in terms

949 of general climate is valid because the source locations for the analysed specimens are  
950 at least 50 km from the contemporary shoreline, and hence not comparable with those  
951 present-day shallow settings close to the coast in the SAB where benthic seasonal  
952 temperature range exceeds 15 °C (see above). Local shallow areas distant from the  
953 SAB coastline have a much lower seasonal range in surface temperature (e.g., 11 °C  
954 at Frying Pan Shoals, about 50 km offshore from Cape Fear; Table 2, stations FPSN7,  
955 41013) and the benthic range is almost certainly a little lower still.

956 When calculated separately for each of the Moore House locations, the seasonal  
957 mean temperatures for Yadkin Pit are higher than for Riddick Pit – only slightly in  
958 summer (respectively,  $28.6 \pm 1.3$  °C and  $26.5 \pm 0.8$  °C) but quite markedly in winter  
959 (respectively,  $14.1 \pm 0.6$  °C and  $9.8 \pm 0.8$  °C). Given the more offshore position of the  
960 former site, it is tempting to think of this as a reflection of Gulf Stream influence.

961 However, the large seasonal range (14.5 °C) argues against this. It therefore seems  
962 likely that the specimens from the two locations are not exactly contemporaneous and  
963 reflect fluctuations in general climate (albeit smaller than the overall change over the  
964 duration of the Yorktown Formation) during deposition of the Moore House Member.

965

966 *Overview.*—The above isotopic data from scallops confirms the mid-Pliocene  
967 warming of marine climate on the eastern seaboard of the US that has been adduced  
968 from other evidence, and shows that warming also occurred in the early Pliocene.

969 Evidence of a benthic seasonal range in excess of 15 °C from the mid-Pliocene  
970 Rushmere and Moore House members indicates that warming was brought about by a  
971 change in general climate rather than an increase in warm-current influence. Indeed,  
972 shallow or emergent areas south of the depositional basin make it hard to countenance  
973 greater warm-current influence. In so far as the benthic seasonal ranges determined

974 for the mid-Pliocene of Virginia are as great as the present surface range in the outer  
975 MAB (Table 1, station 44014), and only a little short of the surface range nearer  
976 shore, it may be concluded that the cold-current influence on this area now, which has  
977 also been inferred for the early Pliocene (*Placopeecten* data), existed additionally in  
978 the mid-Pliocene. While the envisaged current pattern is like that inferred for the early  
979 Pliocene (Fig. 8), the shelf current would have been displaced eastwards during  
980 deposition of the Moore House Member, when sea level was lower (Fig. 2).

981

982 Data from *Mercenaria*

983

984 Winkelstern et al. (2013) obtained  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  profiles from the hinge plates of  
985 six specimens of the infaunal bivalve *Mercenaria*, collected from the Rushmere  
986 Member at a location on the James River, Virginia, approximately the same as that of  
987 the *Chesapecten madisonus* specimen from the Rushmere Member discussed above (6  
988 in Fig. 2B). Three of the specimens (FB5, FB16, FB25; Winkelstern et al., 2013, fig.  
989 6H, 6J, 6L) show a clear antiphase relationship between  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ , suggesting a  
990 shallow-water setting, unlike that inferred for the Rushmere Member in general.

991 Winkelstern et al. (2013) did not tabulate values of maximum and minimum  $\delta^{18}\text{O}$   
992 from each shell but listed winter (15.7 °C, 15.3 °C, 20.2 °C, 16.5 °C, 18.6 °C, 15.5  
993 °C) and summer (24.7 °C, 25.8 °C, 27.7 °C, 26.0 °C, 29.2 °C, 23.7 °C) temperatures  
994 calculated from these data using an equation appropriate for the aragonite mineralogy  
995 of *Mercenaria* (Grossman and Ku, 1986) and a value for  $\delta^{18}\text{O}_{\text{seawater}}$  of +1.1‰  
996 (reduced by 0.27‰ for temperature calculation; see above). The temperatures can  
997 thus be directly compared with those calculated from mid-Pliocene scallop data using  
998 the same value for  $\delta^{18}\text{O}_{\text{seawater}}$ . The summer temperature (29.3 °C) obtained from the

999 single investigated Rushmere scallop is higher than any obtained from *Mercenaria*  
1000 and the winter temperature (13.3 °C) is lower. The winter temperature (12.5 °C) from  
1001 the single investigated Morgarts Beach scallop is similarly lower, as are all the winter  
1002 temperatures (8.9–14.5 °C) from the six Moore House scallops. The summer  
1003 temperatures from the Moore House scallops (25.3–29.8 °C) overlap the range of  
1004 *Mercenaria* data but the mean of the former ( $27.6 \pm 1.5$  °C;  $\pm 1\sigma$ ) is a little higher  
1005 than the mean from the *Mercenaria* data ( $26.2 \pm 1.8$  °C), while the winter mean from  
1006 the Moore House scallops ( $12.0 \pm 2.2$  °C) is substantially lower than from *Mercenaria*  
1007 ( $17.0 \pm 1.8$  °C). Although the *Mercenaria* data agrees with that from mid-Pliocene  
1008 scallops in that it demonstrates higher winter and summer benthic temperatures (and a  
1009 higher median temperature: 21.6 °C) than in the early Pliocene, it differs radically by  
1010 evincing a low seasonal range (9.2 °C). Irrespective of the fact that a higher surface  
1011 range can be inferred if the shells derive from a stratified setting (as seems probable  
1012 for the Rushmere Member in general but is contradicted by the  $\delta^{18}\text{O}/\delta^{13}\text{C}$  evidence  
1013 from these shells), the figure for benthic range (which is well short of the test criterion  
1014 of 15 °C) argues against the model of general climatic warming and continuing cold-  
1015 current influence adduced above. Indeed, Winkelstern et al. (2013) argue perfectly  
1016 logically from their data that the mid-Pliocene warming of marine climate on the  
1017 eastern US seaboard was a consequence of increased warm-current influence.

1018 The low benthic seasonal range identified by Winkelstern et al. (2013) results  
1019 largely from the relatively high winter temperatures determined from their  $\delta^{18}\text{O}$   
1020 profiles. It is possible that these are an artefact of growth in a setting influenced by  
1021 winter freshwater influxes; this would have reduced shell  $\delta^{18}\text{O}$ , resulting in an  
1022 overestimate of winter temperature. While the Rushmere Member was undoubtedly  
1023 deposited in an offshore, fully marine setting, it is conceivable that some faunal

1024 elements were transported from a nearer shore, freshwater-influenced environment.  
1025 Certainly *Mercenaria* is able to tolerate reduced salinity (Elliot et al., 2003) and the  
1026  $\delta^{18}\text{O}/\delta^{13}\text{C}$  evidence from the Rushmere specimens is consistent with growth in a  
1027 nearshore setting. Many (but not all) individuals from the shell bed concerned are  
1028 disarticulated and broken (I.Z. Winkelstern, personal communication, 2016),  
1029 suggesting a measure of transport. However, it is questionable whether the shells  
1030 could have been moved offshore the many tens of kilometers implied from near the  
1031 contemporary shoreline (Fig. 2), especially as storm currents (the only plausible  
1032 agent) have a weaker offshore than alongshore component (Swift et al., 1986).

1033 An alternative explanation for the winter temperatures from Rushmere *Mercenaria*  
1034 is that growth slowed during that season and sampling was insufficiently close to  
1035 identify winter extremes of shell  $\delta^{18}\text{O}$ . In modern *Mercenaria* the optimum  
1036 temperature for growth is about 20 °C, and in most populations growth is significantly  
1037 reduced at temperatures below the minimum (15.3 °C) recorded by Rushmere forms,  
1038 although it may continue to 9 °C (Ansell, 1968). The reduction in growth with  
1039 declining temperature seems a likely explanation for the relatively low winter values  
1040 of shell  $\delta^{18}\text{O}$ , compared to those predicted, in modern forms from Cedar Key, Florida,  
1041 where water temperature does not fall below 10 °C (Elliot et al., 2003, figs. 2, 7). The  
1042 possibility of a combined growth rate/sampling effect on the winter temperatures  
1043 supplied by Rushmere forms is borne out by a comparison of the data of Winkelstern  
1044 et al. (2013) from *Mercenaria* of the early Pleistocene Chowan River Formation with  
1045 that of Krantz (1990) from *Carolinapecten eboreus* of the same unit. The former was  
1046 obtained, like the data from Rushmere *Mercenaria*, by sampling the hinge plate, while  
1047 the latter derives from sampling the full shell along the axis of maximum growth,  
1048 providing better temporal resolution even at the greater sample spacing (~1 mm

1049 compared to ~0.1 mm). The mean of maximum summer temperatures from six  
1050 Chowan River *Mercenaria* (Winkelstern et al., 2013, p. 655; calculated with  
1051  $\delta^{18}\text{O}_{\text{seawater}} = 0.0\text{‰}$ ) is  $22.0 \pm 2.2$  °C, similar to the mean of  $20.8 \pm 1.9$  °C derived  
1052 from eight Chowan River *C. eboreus* calculated using data for minimum shell  $\delta^{18}\text{O}$   
1053 (Krantz et al., 1990, table 4), the same value for  $\delta^{18}\text{O}_{\text{seawater}}$ , and Equation 1. By  
1054 contrast, the equivalent winter temperature from Chowan River *Mercenaria* is  $10.5 \pm$   
1055  $0.5$  °C while that from *C. eboreus* is  $7.5 \pm 1.6$  °C, and it should be noted that the latter  
1056 figure is probably something of an overestimate because four of the shells used have  
1057 major growth breaks close to the position of the samples yielding the highest value of  
1058  $\delta^{18}\text{O}$  (Krantz, 1990, figs. 6, 7). Notwithstanding this confirmation of differences  
1059 between estimates of winter temperature from the full shell of scallops and the hinge  
1060 plate of *Mercenaria*, it should be noted that at least some of the *Mercenaria* profiles  
1061 (both from the Rushmere Member and the Chowan River Formation) have well-  
1062 resolved ('sinusoidal') winter portions, and a profile obtained from the full shell of  
1063 one *Mercenaria* specimen shows winter (and summer) extreme values very similar to  
1064 those in an equivalent profile from the hinge plate (Winkelstern et al., 2013, fig. 5).  
1065 Moreover, while some of the winter sectors of Chowan River *Mercenaria* profiles  
1066 correspond to dark shell material (usually associated with slow growth), others  
1067 correspond to light shell material, and this is generally the case for Rushmere shells,  
1068 arguing for relatively fast growth in winter.

1069 While certain possibilities require further investigation, there is at present nothing  
1070 to invalidate the temperature data from Rushmere *Mercenaria*. One must therefore  
1071 accept that these lived at a time when winter temperature was higher than that  
1072 experienced by the investigated mid-Pliocene scallops, and that this resulted from

1073 warm-current influence, probably in addition to the effect of general climatic  
1074 warming.

1075

1076 SEASONAL TEMPERATURE RANGE FOR THE HIGHER YORKTOWN  
1077 FORMATION FROM BRYOZOAN ZOOID SIZE

1078

1079 Knowles et al. (2009) measured variation in the size of zooids through the growth  
1080 (astogeny) of colonies of various cheilostome bryozoan species to obtain estimates of  
1081 mean annual range in temperature (MART) for the Rushmere ( $6.39 \pm 0.69$  °C;  $\pm 1\sigma$ ),  
1082 Morgarts Beach ( $6.54 \pm 1.24$  °C) and Moore House ( $6.39 \pm 0.96$  °C) members in  
1083 Virginia. These estimates are very much lower than the figures for seasonal  
1084 temperature range obtained by isotopic analysis of scallops and also lower than the  
1085 figure obtained by isotopic analysis of *Mercenaria*. The bryozoan MART technique is  
1086 generally robust (Okamura et al., 2011), and the colonies analysed by Knowles et al.  
1087 (2009) did not apparently contain any growth breaks which would have led to  
1088 underestimates of seasonal range, so on the face of it one must take these results as a  
1089 further indication of the periodic influence of warm currents in the mid-Pliocene of  
1090 Virginia. However, the maps of average monthly benthic temperature supplied by  
1091 Atkinson et al. (1983) show that in the shelf region at present influenced by warm  
1092 currents on the eastern seaboard of the USA only a small area of the outer shelf within  
1093 the southern SAB experiences a seasonal range in benthic temperature as low as that  
1094 indicated by bryozoans for the mid-Pliocene in Virginia. While there are some  
1095 uncertainties about the depth and distance from shore at which the sequences  
1096 concerned accumulated, it is unlikely that they represent outer shelf settings, so it is  
1097 questionable whether the figures supplied by the bryozoan MART technique are

1098 accurate in this case. One way of testing would be to obtain oxygen isotope profiles  
1099 across the colonies, although extracting samples which are not time-averaged would  
1100 be difficult in species exhibiting secondary skeletal wall thickening (Knowles et al.,  
1101 2010). Until confirmatory isotopic evidence is provided we feel that the figures for  
1102 seasonal temperature range from zooid-size variation in Yorktown Formation  
1103 bryozoans cannot be accepted.

1104

#### 1105 CONCLUSIONS AND FURTHER WORK

1106

1107 New oxygen isotope data presented herein from the scallop *Placopecten clintonius*  
1108 of the early Pliocene Sunken Meadow Member (Yorktown Formation) confirms other  
1109 indications of a relatively cool marine climate at this time on the US eastern seaboard  
1110 in the area of Virginia and North Carolina. The uniformity of cool conditions over this  
1111 region is most simply interpreted as a consequence of greater southward penetration  
1112 of cold currents in the absence of a feature analogous to Cape Hatteras. This  
1113 interpretation is supported by evidence of high primary productivity, which could  
1114 have been promoted by supply of nutrient-rich cold water from the north. Reanalysis  
1115 of existing oxygen isotope data from other scallop taxa confirms previous reports of a  
1116 warming of marine climate in the mid-Pliocene but indicates that this was not due to  
1117 the impingement of warm currents but to a warming of general climate, with cold  
1118 currents still penetrating the area. Existing oxygen isotope data from examples of the  
1119 infaunal bivalve *Mercenaria* from the mid-Pliocene Rushmere member of the  
1120 Yorktown Formation suggests otherwise. The warm-current influence indicated by the  
1121 high median temperature and low seasonal range derived from these shells probably  
1122 reflects a temporary increase in the vigour of the Gulf Stream rather than a switch

1123 from an ‘off’ to an ‘on’ state. The former state may have existed in marine isotope  
1124 stage M2 (~3.3 Ma; Lisiecki and Raymo, 2005), when there is evidence of extensive  
1125 glaciation in the northern hemisphere, but during the subsequent MPWP the Gulf  
1126 Stream was probably continuously ‘on’ (De Schepper et al., 2013). While local  
1127 topographic change might have allowed Gulf Stream water to temporarily displace  
1128 water derived from the north on the shelf of the eastern USA, the evidence of Pliocene  
1129 fluctuations in warm-current influence derived from isotopic and other indications of  
1130 temperature on the other side of the North Atlantic (Fig. 1; Johnson et al., 2009;  
1131 Knowles et al., 2009; Williams et al., 2009; Valentine et al., 2011) indicates the  
1132 likelihood of regional oceanographic change, e.g., in the strength and position of the  
1133 North Atlantic gyre, of which the Gulf Stream is part.

1134       Clearly, there is a need for data from co-occurring, autochthonous bivalves and  
1135 bryozoans from the mid-Pliocene of the eastern USA to determine whether the  
1136 divergent estimates of seasonal temperature range from isotopic analysis of the former  
1137 and zooid-size analysis of the latter are a reflection of inaccuracies in one or other  
1138 approach, or representative of real differences resulting from temporal variation in  
1139 warm-current influence. If congruent data are obtained, it will be useful to chart  
1140 stratigraphic changes in seasonality in greater detail and to investigate whether there  
1141 is a matching pattern on the other side of the Atlantic, and hence a common cause.  
1142 Insights into the controls on marine climate in the North Atlantic region are likely to  
1143 be derived from investigations into primary productivity, since this is dependent on  
1144 nutrient supply, which is in turn influenced by current patterns. Indications of primary  
1145 productivity can be obtained from sediment composition, and from the abundance,  
1146 diversity and type of the fossil biota (see above). However, they can also be obtained  
1147 from shell profiles of indicative trace elements (Krantz et al., 1988; Haveles et al.,

1148 2010; Thébault and Chauvaud, 2013) and from evidence of shell growth rates (Kirby,  
1149 2000, 2001; Johnson et al., 2007; Haveles et al., 2010). In the latter respect it is of  
1150 interest that Goewert and Surge (2008) recorded extensional growth rates up to nearly  
1151 70 mm per annum in their specimens of *Chesapecten madisonius* from the Moore  
1152 House Member. This is similar to the maximum annual growth rate in wild modern  
1153 scallops (Yamamoto, 1953; Bricelj and Shumway, 1991, fig. 7) and certainly implies  
1154 an abundant food source, probably phytoplankton. Other bivalve taxa (e.g.,  
1155 *Carolinapecten*, *Mercenaria*, *Glycymeris*, *Marvacrassatella*, *Dinocardium*) reach a  
1156 large size in the Yorktown Formation and may likewise have grown rapidly.  
1157 Sclerochronological techniques provide a means of testing this.

1158

1159

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1177

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1497

1498 FIGURE CAPTIONS

1499

1500 FIG. 1.—Stratigraphy of the Yorktown Formation and correlative formations in the  
1501 southern North Sea Basin, based on Krantz (1991), Williams et al. (2009), De  
1502 Schepper et al. (2009), Winkelstern et al. (2013) and discussion herein (ages in Ma;  
1503 MPWP = Mid-Pliocene/Piacenzian Warm Period). Note that Winkelstern et al. (2013)  
1504 placed the Moore House Member after the MPWP (3.29-2.97 Ma) on the basis of Sr  
1505 isotope dating but Krantz (1991) related it to a phase of warming and global ice-  
1506 volume reduction identified in the deep-ocean  $\delta^{18}\text{O}$  record at 3.1-3.0 Ma. Williams et  
1507 al. (2009) placed the Rushmere Member before the MPWP but since it and the  
1508 succeeding Morgarts Beach Member are representative of the same major  
1509 transgression we consider, like Winkelstern et al. (2013), that at least part of the  
1510 Rushmere Member must fall within the MPWP. Asterisks indicate units for which  
1511 there are existing isotopic paleotemperature determinations (Krantz, 1990; Goewert

1512 and Surge, 2008; Johnson et al., 2009; Williams et al., 2009; Valentine et al., 2011;  
1513 Winkelstern et al. 2013).

1514

1515 FIG. 2.—Geography and Pliocene paleogeography of study area, and sample sites. **A)**  
1516 Surface currents adjacent to the eastern US seaboard at present, principally based on  
1517 Cronin (1988), Csanady and Hamilton (1988) and Böhm et al. (2006). Thick red  
1518 arrow = Gulf Stream (strong, warm); thin red arrow = Carolina Coastal Current  
1519 (weak, warm); thin blue arrows = (left) Virginia Coastal Current (weak, cool) and  
1520 (right) ‘slope current’ (weak, cool); □ 200m contour included to show position of  
1521 shelf edge. **B)** Enlargement of area indicated by box in A, with positions of Sunken  
1522 Meadow (brown), Rushmere/Morgarts Beach (mauve) and Moore House (green)  
1523 shorelines according to Ward et al. (1991). Numbers indicate collection locations  
1524 referred to herein (coloured to match the relevant shoreline): 1 = Grove Wharf; 2 =  
1525 Claremont; 3 = Lee Creek Mine, Aurora; 4 = Sunken Meadow Creek; 5 = Kingsmill;  
1526 6 = Fort Boykin, Burwell Bay; 7 = Lieutenant Run, Petersburg; 8 = Riddick Pit,  
1527 Chuckatuck; 9 = Yadkin Pit, Deep Creek. Note that location 2 is actually closer to  
1528 Sunken Meadow Creek than location 4. Locations 1, 2, 3, 4, 5 and 7 correspond to  
1529 localities 31, 7, 49, 42, 81 and 43, respectively, of Ward and Blackwelder (1980).  
1530 Location 6 is midway between localities 55 and 61 of Ward and Blackwelder (1980).  
1531 Goewert and Surge (2008) and Ward (1989) provide sedimentary logs for locations 8  
1532 and 9, respectively.

1533

1534 FIG. 3.—Morphology of *Placopecten clintonius*. **A)** Specimen NC1, showing the  
1535 positions of major (filled triangles) and moderate (open triangles) growth breaks  
1536 indicated in Figs. 4E and 6E. **B)** Microgrowth increments in the mid-ventral sector of

1537 specimen VA2 (filled triangle identifies the major growth break at 68 mm shell height  
1538 indicated in Figs. 4B and 6B). Scale bars = 10 mm.

1539

1540 FIG. 4.—Oxygen isotope (red line), carbon isotope (black line) and microgrowth  
1541 increment (blue line) data from *Placopecten clintonius* specimens from the Sunken  
1542 Meadow Member of Virginia (**A-D**) and North Carolina (**E-H**). Isotopic axis reversed  
1543 so that lower values of  $\delta^{18}\text{O}$  (representative of higher temperatures) plot towards the  
1544 top. Thin, dashed blue lines = raw increment data; thicker, continuous blue lines =  
1545 five-point averages. Filled blue triangles = major growth breaks; open blue triangles =  
1546 moderate growth breaks (indicated by a less pronounced ‘step’ in the shell profile).  
1547 S1, S2... and W1, W2... refer respectively to summers and winters as identified from  
1548 the  $\delta^{18}\text{O}$  profiles. Stars = anomalous values which are excluded from subsequent  
1549 analysis (see text for explanation). Exclusion of the two anomalous values in C has  
1550 the effect of making the immediately preceding value representative of S2 (see Fig.  
1551 6C for clarification).

1552

1553 FIG. 5.—Patterns of variation in microgrowth increment size in *Aequipecten*  
1554 *opercularis*. **A**) Three individuals (blue, green and yellow lines) from a seasonally  
1555 stratified setting (50 m depth) in the Gulf of Tunis, Mediterranean Sea. **B**) Three  
1556 individuals (blue, green and yellow lines) from the continuously well-mixed waters of  
1557 the southern North Sea. Plots are five-point averages of the raw data, which has been  
1558 excluded for purposes of clarity. Red lines =  $\delta^{18}\text{O}$  profiles from the specimens  
1559 providing the blue increment profiles in A and B (data from Johnson et al., 2009, figs.  
1560 5, 4C, respectively). Profiles of  $\delta^{18}\text{O}$  for the specimens providing the green and  
1561 yellow increment profiles in B are given in Johnson et al. (2009, fig. 4B, 4D,

1562 respectively) but are not available for the specimens providing the green and yellow  
1563 profiles in A. The scales of the axes are the same as those of Figure 4 to facilitate  
1564 comparison (note, however, that the bounds of the increment height axes differ).  
1565 Specimens represented in A are: blue increment profile (and  $\delta^{18}\text{O}$  profile), Muséum  
1566 National d'Histoire Naturelle, Paris (MNHN) IM-2008-1537; green increment profile,  
1567 MNHN IM-2008-1539; yellow increment profile, MNHN IM-2008-1538. Specimens  
1568 represented in B are: blue increment profile (and  $\delta^{18}\text{O}$  profile), British Geological  
1569 Survey (BGS), Zt 9955; green increment profile, BGS Zt 9953; yellow increment  
1570 profile, BGS Zt 9957.

1571

1572 FIG. 6.—Temperature profiles from *Placopecten clintonius* specimens from the  
1573 Sunken Meadow Member of Virginia (**A-D**) and North Carolina (**E-H**), calculated  
1574 using the data in Figure 4 (anomalous points excluded), Equation 1 and values for  
1575  $\delta^{18}\text{O}_{\text{seawater}}$  of  $\square 0.4\text{‰}$ ,  $+0.7\text{‰}$  and  $+1.1\text{‰}$  (respectively, lower, middle and upper lines  
1576 in each plot). The preferred profiles ( $\delta^{18}\text{O}_{\text{seawater}} = +0.7\text{‰}$ ) are indicated by a thicker  
1577 line. Symbols indicating seasonal assignment (S1, S2...; W1, W2...) and growth  
1578 breaks (filled and open blue triangles) are explained in Figure 4. Symbols for growth  
1579 breaks beyond the ventral end of the temperature profile have been excluded from H.

1580

1581 FIG. 7.—False colour satellite images of the Atlantic Ocean off the coast of  
1582 southeastern Canada and the northeastern US (Gulf of Maine to Cape Hatteras),  
1583 showing geographic variation in environmental parameters of surface waters. **A**)  
1584 Temperature. **B**) Concentration of phytoplankton pigments. Data collected on 14 June  
1585 1979 by the Coastal Zone Color Scanner on the Nimbus-7 satellite. In A the warmest  
1586 water (about 25 °C) is shown by orange/red and the coldest (about 6 °C) by dark blue,

1587 with water of intermediate temperature shown by yellow and green; in B the highest  
1588 concentrations of phytoplankton pigment are shown by dark brown and the lowest by  
1589 blue, with intermediate concentrations shown by yellow and green (land is light  
1590 brown and clouds are white or beige). Note the low concentration of phytoplankton  
1591 pigments (implied low primary productivity) in warm, Gulf Stream water (including a  
1592 warm-core eddy east of the Delmarva Peninsula) and the higher concentration of  
1593 phytoplankton pigments typical of the cooler water nearer the shelf (Slope Sea). The  
1594 very high concentration of phytoplankton pigments close to much of the coastline is a  
1595 reflection of nutrient input from the land, itself strongly influenced by human  
1596 activities. Adapted from Colling et al. (2001, fig. 4.31), with permission from  
1597 Elsevier.

1598

1599 FIG. 8.—Envisaged disposition of currents in the area shown in Figure 2B during  
1600 deposition of the basal Sunken Meadow Member. Brown line = position of shoreline  
1601 according to Ward et al. (1991); position of shelf edge is that of present  $\square$  200 m  
1602 contour. The greater southward penetration of cool currents (medium thickness blue  
1603 arrows) on shelf and slope compared to now (Fig. 2A) is explained in the text, as are  
1604 the intrusions of slope water (thin blue arrows) onto the shelf. Arguably, shallows in  
1605 the region of the Mid-Carolina Platform High (see text) may have prevented cool-  
1606 current flow on the shelf as far south as is shown (i.e. into southernmost North  
1607 Carolina). The point of meeting and eastward deflection of the slope current and Gulf  
1608 Stream (thick red arrow) may have been farther south than shown. A similar  
1609 disposition of currents is envisaged during deposition of most of the higher Yorktown  
1610 Formation, but at times the Gulf Stream may have been more vigorous, penetrating  
1611 farther north and influencing marine climate on the shelf (see text).

1612

1613

## TABLE CAPTIONS

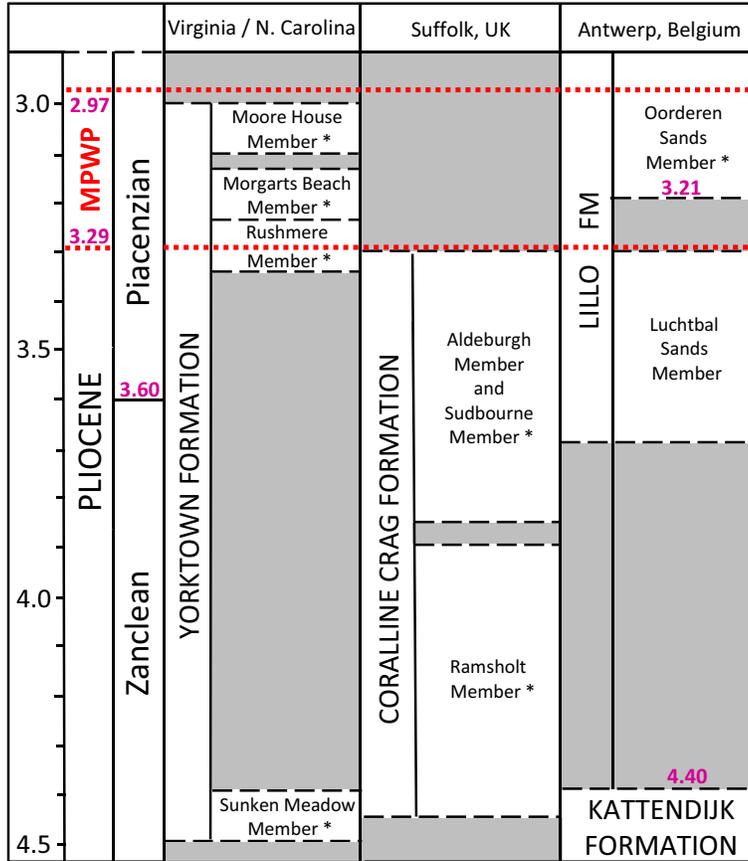
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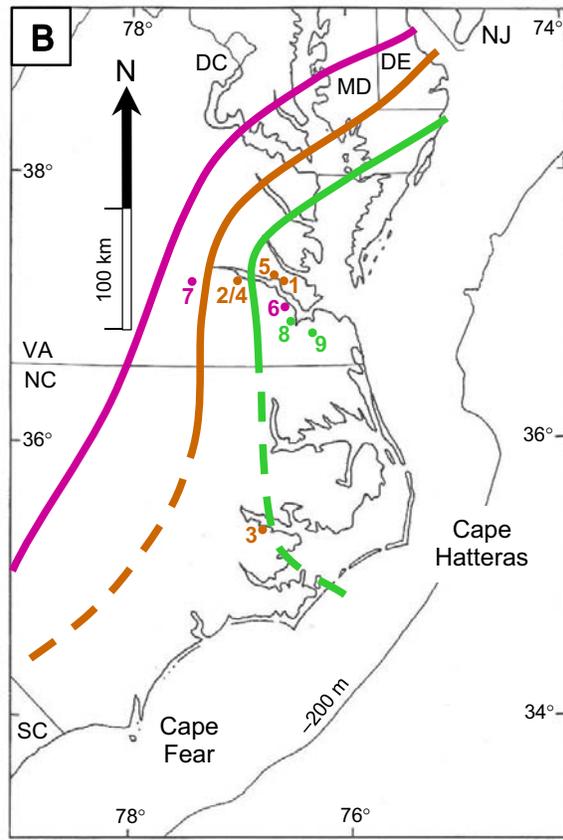
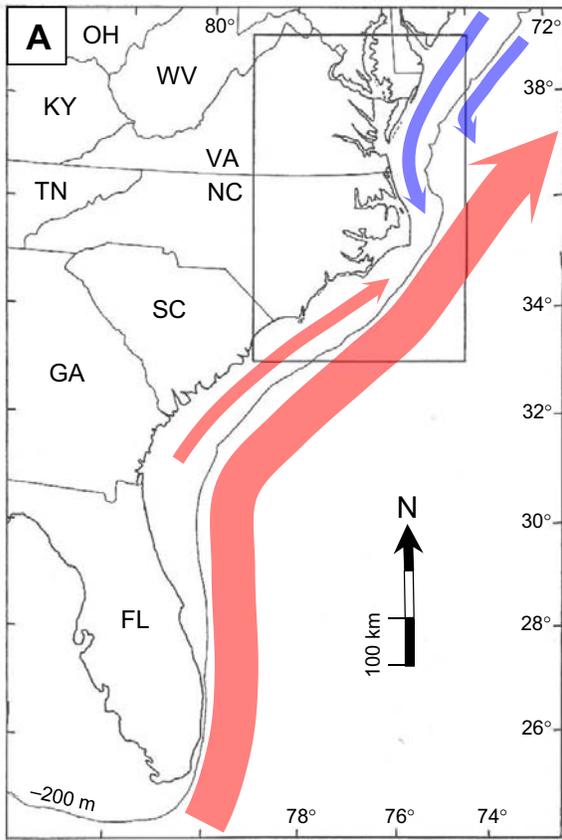
1615 TABLE 1.—Mean winter minimum and mean summer maximum sea-surface  
1616 temperatures, and seasonal ranges, for selected coastal to outer shelf locations up to  
1617 approximately three degrees of latitude north and south of Cape Hatteras. Locations  
1618 listed in order of decreasing latitude. Descriptions of shelf settings refer to relative  
1619 position between the coast and shelf break, not water depth. Minimum and maximum  
1620 temperatures were read from graphs of mean monthly temperature supplied by the  
1621 National Data Buoy Center (NDBC, undated) and are accurate to the nearest whole  
1622 number.

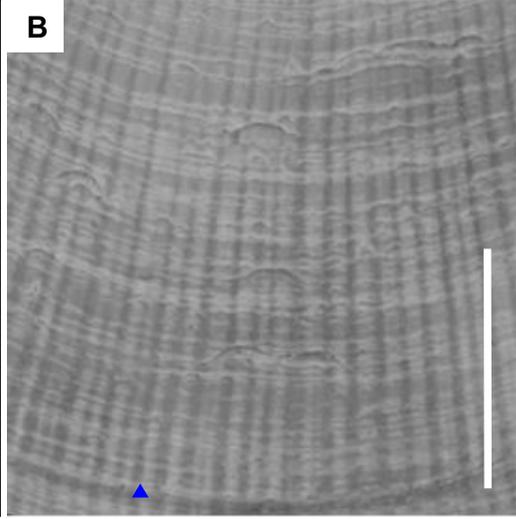
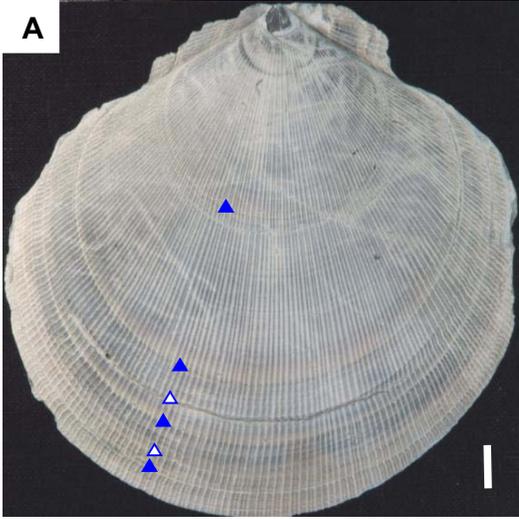
1623

1624 TABLE 2.—Calculated temperatures (°C) for maximum (winter) and minimum  
1625 (summer) values of  $\delta^{18}\text{O}_{\text{calcite}}$  ( $\delta^{18}\text{O}_{\text{c}}$ ; ‰) in scallop specimens from the Yorktown  
1626 Formation, using selected values for  $\delta^{18}\text{O}_{\text{seawater}}$  ( $\delta^{18}\text{O}_{\text{sw}}$ ; ‰). <sup>a</sup> = specimens of  
1627 *Placopecten clintonius* for which raw data are presented herein; <sup>b</sup> = specimens of  
1628 *Chesapecten jeffersonius* (CJ), *C. madisonius* (CM) and *Carolinapecten eboreus* (EB)  
1629 for which raw data are given by Krantz (1990), and <sup>c</sup> = specimens of *C. madisonius*  
1630 (CMAD) for which raw data are given by Goewert and Surge (2008). The  $\delta^{18}\text{O}$  values  
1631 for *Chesapecten* and *Carolinapecten* are the extreme maxima and minima from the  
1632 shells concerned as given in Krantz (1990, table 3) and Goewert and Surge (2008,  
1633 table 2). These values have been assigned to a particular winter or summer by  
1634 reference to the full  $\delta^{18}\text{O}$  profiles supplied by these authors. The Summer 1 values  
1635 from NC2, SM-CJ1 and LTRUN-EB are considered to be from incomplete summer  
1636 records and have been handled accordingly (see text). The Summer 2 value from

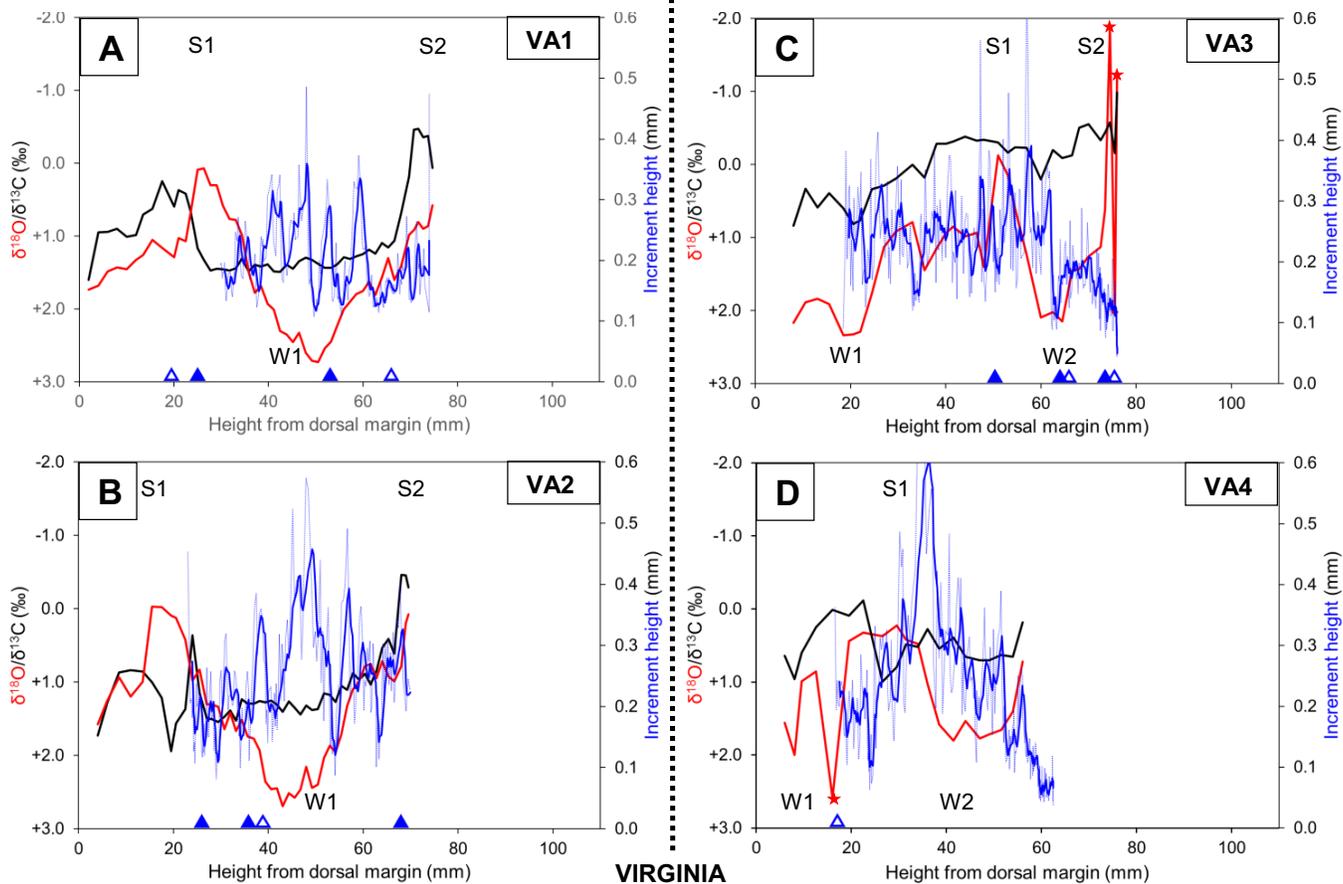
1637 CMAD-4 has been corrected to agree with the corresponding profile (Goewert and  
1638 Surge, 2008, fig. 3b).





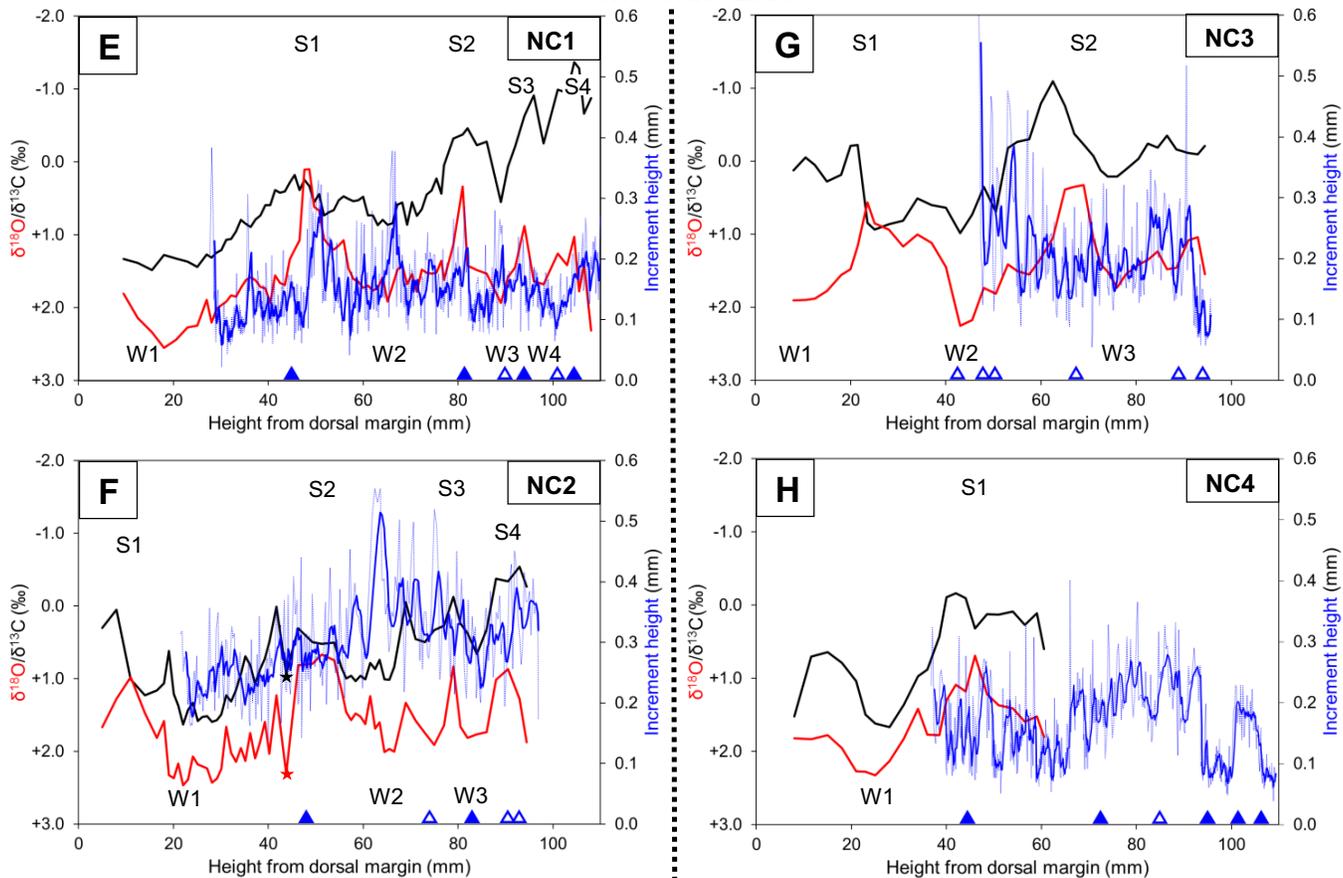


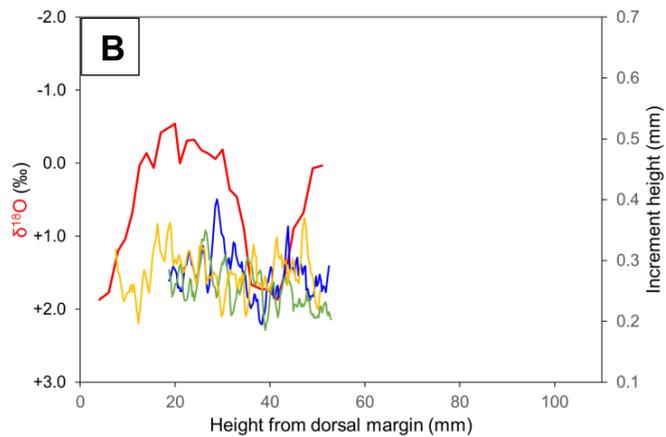
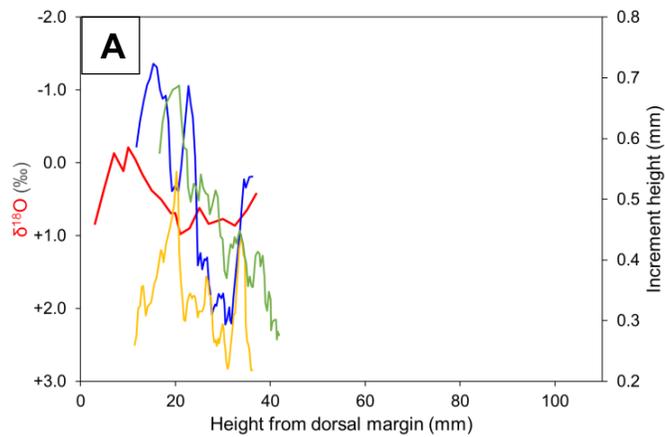
**'FINE' SAMPLING      'COARSE' SAMPLING**



**VIRGINIA**

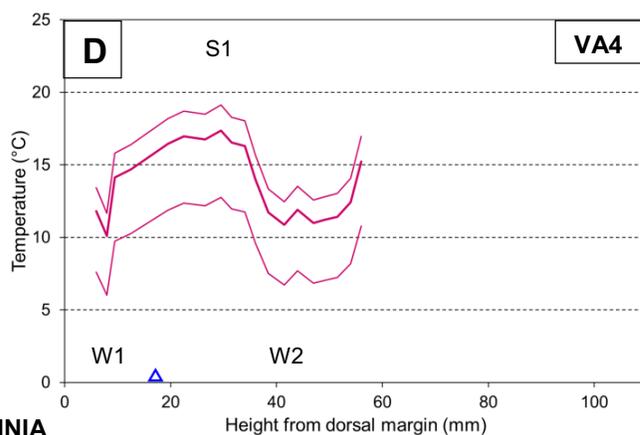
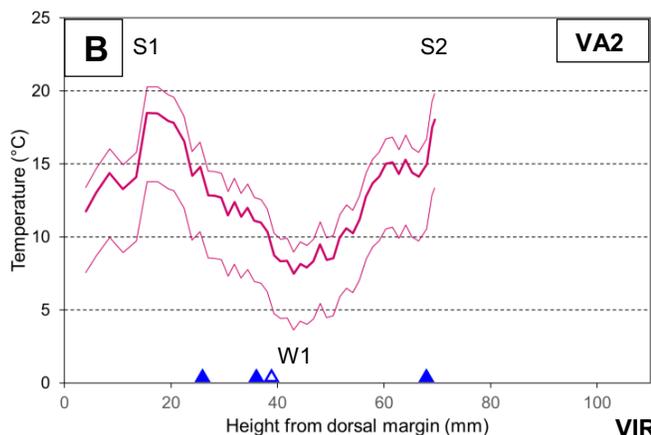
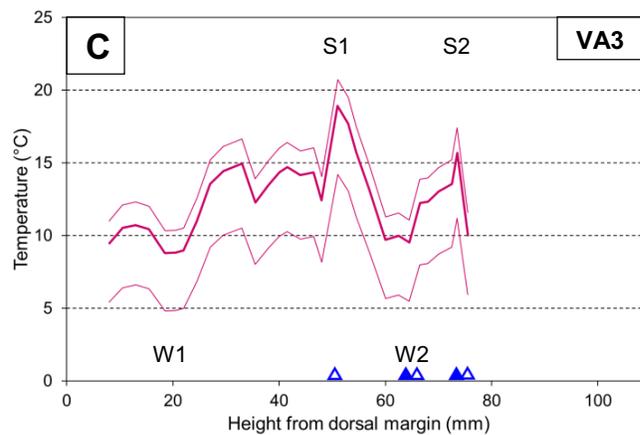
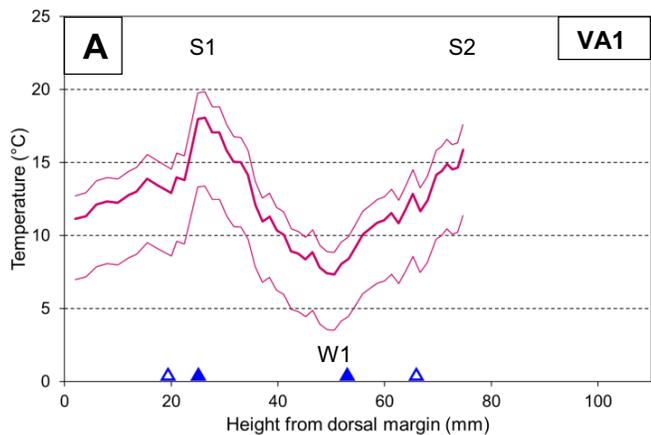
**NORTH CAROLINA**





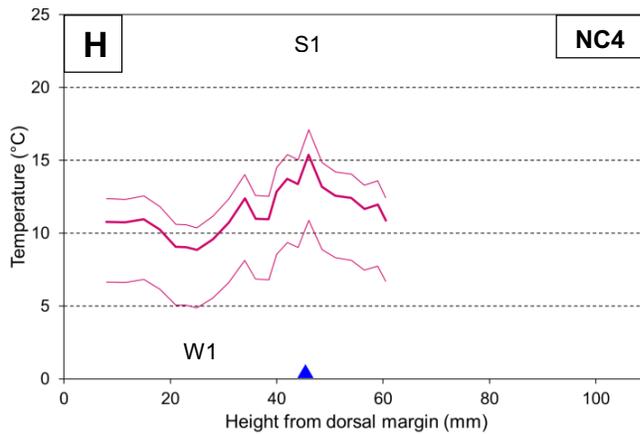
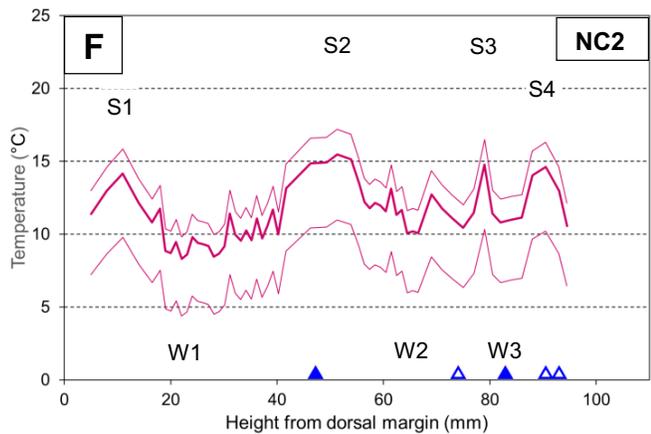
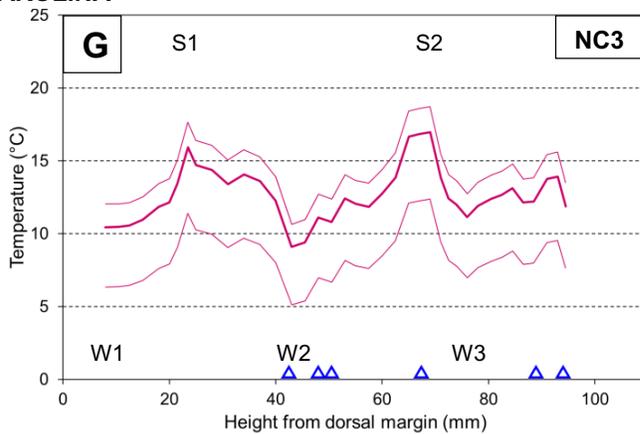
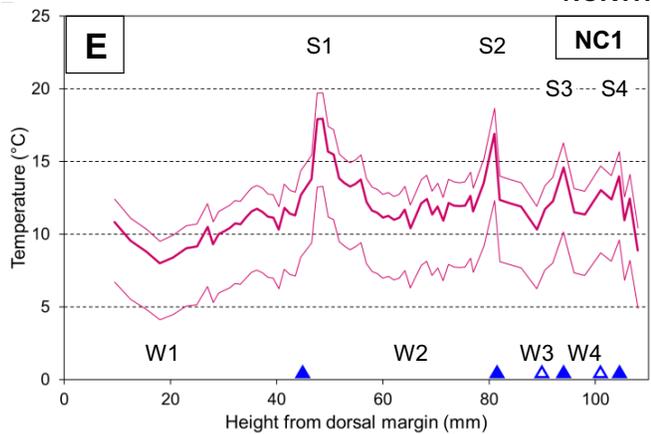
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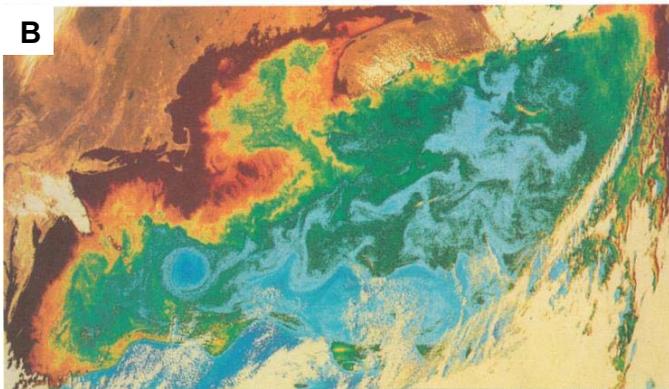
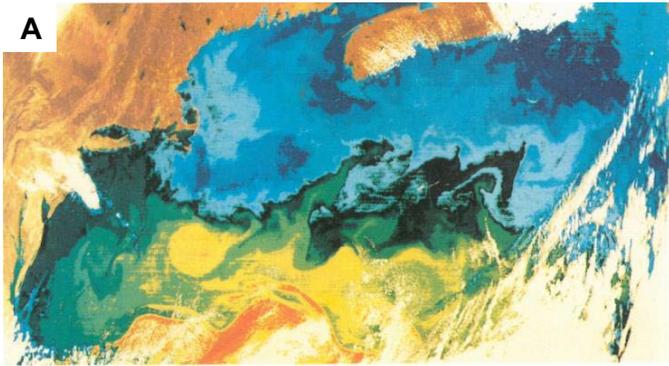
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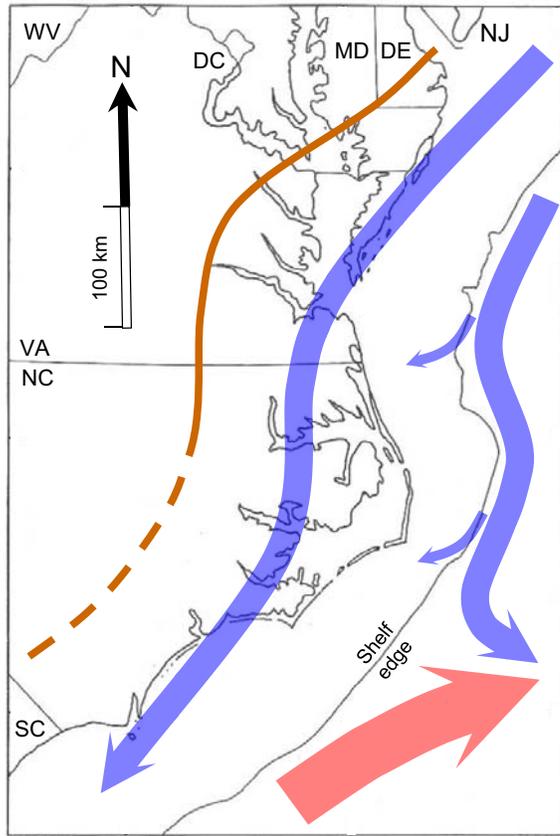


**VIRGINIA**

**NORTH CAROLINA**







Station code	Setting	Latitude and longitude	Period of records	Minimum temp. (°C)	Maximum temp. (°C)	Range in temp. (°C)
44009	Inner shelf	38.5° N 74.7° W	1984-2008	5	23	18
OCIM2	Shore	38.3° N 75.1° W	2008-2012	5	24	19
KPTV2	Shore	37.2° N 76.0° W	2005-2012	5	26	21
CBBV2	Estuary	37.0° N 76.1° W	2005-2012	6	26	20
CHLV2	Inner shelf	36.9° N 75.7° W	1984-2005	6	25	19
44014	Outer shelf	36.6° N 74.8° W	1990-2008	9	25	16
44006	Mid-shelf	36.3° N 75.4° W	1980-1995	6	25	19
DUCN7	Shore	36.2° N 75.7° W	1997-2008	7	24	17
ORIN7	Shore	35.8° N 75.5° W	2005-2012	8	27	19
CAPE HATTERAS		35.3° N 75.5° W				
DSL7	Mid-shelf	35.2° N 75.3° W	1984-2001	15	27	12
41025	Mid-shelf	35.0° N 75.4° W	2003-2008	16	28	12
JMPN7	Shore	34.2° N 77.8° W	2006-2012	11	28	17
41036	Mid-shelf	34.2° N 76.9° W	2006-2008	15	28	13
MROS1	Shore	33.7° N 78.9° W	2005-2012	10	29	19
FPSN7	Mid-shelf	33.5° N 77.6° W	1984-1996	17	28	11
41013	Mid-shelf	33.4° N 77.7° W	2003-2008	17	28	11
SCIS1	Shore	32.9° N 79.7° W	2006-2008	13	29	16
41004	Inner shelf	32.5° N 79.1° W	1978-2008	18	28	10
FRPS1	Shore	32.3° N 80.5° W	2006-2008	12	29	17

Member and shell ID	Winter 1			Winter 2				Summer 1			Summer 2					
	$\delta^{18}\text{O}_c$	Temperature			$\delta^{18}\text{O}_c$	Temperature			$\delta^{18}\text{O}_c$	Temperature			$\delta^{18}\text{O}_c$	Temperature		
		$\delta^{18}\text{O}_{sw}$ □0.4	$\delta^{18}\text{O}_{sw}$ +0.7	$\delta^{18}\text{O}_{sw}$ +1.1												
Sunken Meadow																
VA1 <sup>a</sup>	+2.73	3.5	7.3	8.8	-	-	-	-	+0.07	13.4	18.1	19.9	+0.57	11.4	15.9	17.6
VA2 <sup>a</sup>	+2.69	3.6	7.5	9.0	-	-	-	-	□0.03	13.8	18.5	20.3	+0.08	13.4	18.0	19.8
VA3 <sup>a</sup>	+2.34	4.8	8.8	10.3	+2.15	5.5	9.5	11.1	□0.13	14.2	18.9	20.7	+0.62	11.2	15.7	17.4
VA4 <sup>a</sup>	+2.00	6.0	10.1	11.7	+1.80	6.7	10.9	12.5	+0.23	12.8	17.4	19.1	-	-	-	-
NC1 <sup>a</sup>	+2.55	4.1	8.0	9.5	+1.91	6.3	10.4	12.0	+0.10	13.3	17.9	19.7	+0.34	12.3	16.9	18.7
NC2 <sup>a</sup>	+2.47	4.4	8.3	9.8	+2.01	6.0	10.1	11.7	+0.98	9.8	14.2	15.9	+0.67	11.0	15.5	17.2
NC3 <sup>a</sup>	+1.90	6.4	10.5	12.0	+2.25	5.1	9.1	10.7	+0.56	11.4	15.9	17.7	+0.32	12.4	17.0	18.7
NC4 <sup>a</sup>	+2.33	4.9	8.9	10.4	-	-	-	-	+0.69	10.9	15.4	17.1	-	-	-	-
KING-CJ <sup>b</sup>	-	-	-	-	+1.5	7.8	12.1	13.7	□1.2	18.8	23.9	25.8	-	-	-	-
SM-CJ1 <sup>b</sup>	+1.9	6.4	10.5	12.1	-	-	-	-	□0.3	14.9	19.7	21.5	-	-	-	-
SM-CJ2 <sup>b</sup>	-	-	-	-	+1.6	7.5	11.7	13.3	□0.8	17.1	22.0	23.9	-	-	-	-

Rushmere																	
BB-CM <sup>b</sup>	+1.6	7.5	11.7	13.3	-	-	-	-	-	-	-	-	-	□1.9	22.0	27.3	29.3
Morgarts Beach																	
LTRUN-EB <sup>b</sup>	+1.8	6.7	10.9	12.5	-	-	-	-	+0.3	12.5	17.1	18.8	-	-	-	-	
Moore House																	
YAD-CM1 <sup>b</sup>	+1.6	7.5	11.7	13.3	-	-	-	-	□1.9	22.0	27.3	29.3	-	-	-	-	
YAD-CM2 <sup>b</sup>	+1.3	8.6	12.9	14.5	-	-	-	-	□2.0	22.5	27.8	29.8	-	-	-	-	
YAD-EB1 <sup>b</sup>	+1.3	8.6	12.9	14.5	-	-	-	-	□1.4	19.7	24.8	26.8	-	-	-	-	
CMAD-2 <sup>c</sup>	+2.7	3.6	7.5	8.9	-	-	-	-	□1.4	19.7	24.8	26.8	-	-	-	-	
CMAD-4 <sup>c</sup>	+2.5	4.3	8.2	9.7	-	-	-	-	-	-	-	-	□1.5	20.2	25.3	27.3	
CMAD-5 <sup>c</sup>	+2.2	5.3	9.3	10.9	-	-	-	-	-	-	-	-	□1.1	18.4	23.4	25.3	