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**LIFE HISTORY, ENVIRONMENT AND EXTINCTION OF THE SCALLOP
CAROLINAPECTEN EBOREUS (CONRAD) IN THE PLIO-PLEISTOCENE OF THE
US EASTERN SEABOARD**

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RRH: TEMPERATURE VERSUS PRIMARY PRODUCTION IN SCALLOP EXTINCTION

LRH: A.L.A. JOHNSON ET AL.

26 **ABSTRACT: Plio-Pleistocene mass extinction of marine bivalves on the US eastern**
27 **seaboard has been attributed to declines in temperature and primary production. We**
28 **investigate the relationship of growth rate in the scallop *Carolinapecten eboreus* to**
29 **variation in these parameters to determine which contributed to its extinction. We use**
30 **ontogenetic profiles of shell $\delta^{18}\text{O}$ to estimate growth rate and seasonal temperature,**
31 **microgrowth-increment data to validate $\delta^{18}\text{O}$ -based figures for growth rate, and shell**
32 **$\delta^{13}\text{C}$ to supplement assemblage evidence of production. Post-larval growth started in**
33 **the spring/summer in individuals from the Middle Atlantic Coastal Plain but in the**
34 **autumn/winter in some from the Gulf Coastal Plain. Growth rate typically declined**
35 **with age and was usually higher in summer than winter. Many individuals died in**
36 **winter but the largest forms typically died in spring, possibly on spawning for the first**
37 **time. No individuals lived longer than two years and some grew exceedingly fast overall,**
38 **up to 60% more rapidly than any other scallop species (< 145.7 mm in a year). Faster**
39 **growth was generally achieved by secreting more rather than larger microgrowth**
40 **increments. Some very fast-growing individuals lived in settings of high production and**
41 **low temperature. No individuals grew slowly under high production whereas most if not**
42 **all grew slowly under ‘average’ production and low temperature. In that the rapid**
43 **growth evidently enabled by high production would have afforded protection from**
44 **predators, Plio-Pleistocene decline in production was probably contributory to the**
45 **extinction of *C. eboreus*. However, the negative impact of low temperature on growth**
46 **under ‘average’ production suggests that temperature decline played some part.**

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48

INTRODUCTION

49

50 During the Plio-Pleistocene, 45% of marine bivalve mollusk species became extinct in
51 western Europe (Raffi et al. 1985), and 65% in the eastern US (Stanley 1986). The figure for
52 the latter area includes a deduction for the rate of normal/background species loss, as
53 estimated from relatively stable Plio-Pleistocene faunas in the western US and Japan, so
54 species loss in the eastern US can truly be described as a mass extinction. High Plio-
55 Pleistocene loss of marine mollusk species has been documented in the Caribbean area
56 (Jackson et al. 1993; Jackson and Johnson 2000; Smith and Jackson 2009), so evidently an
57 extinction event occurred throughout the North Atlantic region.

58 Bivalve extinction in the North Atlantic region was broadly coincident with the onset of
59 northern hemisphere glaciation, and many warmth-favoring taxa were victims. Consequently,
60 temperature decrease has been proposed as the cause (Stanley and Campbell 1981; Raffi et al.
61 1985; Stanley 1986; Stanley and Ruddiman 1995), with zones of upwelling cold water and
62 (in the eastern US) increased seasonality invoked to explain the failure of warmth-adapted
63 species to survive by migration southwards. An alternative (or supplementary) explanation in
64 terms of a decline in primary production (food supply) has been suggested for the eastern US
65 and Caribbean by Allmon and colleagues (Allmon et al. 1993, 1996; Allmon 2001),
66 supported for the Caribbean by other workers (e.g., Todd et al. 2002), although a lagged
67 response has been noted there (O’Dea et al. 2007). This lag might reflect localised persistence
68 of high primary production (Leigh et al. 2014), indirect action of production decline through
69 its effects on dominant habitat and hence predation intensity (Leonard-Pingel and Jackson
70 2016), or simply the time required for production decline (acting directly or indirectly) to
71 bring about complete extinction (O’Dea and Jackson 2009; Smith and Jackson 2009).

72 As a contribution to debate over the cause of Plio-Pleistocene extinctions amongst marine
73 bivalves in the eastern US, we present in this paper an investigation into the roles of declines
74 in temperature and primary production in the extinction of a single species, the scallop

75 (pectinid) *Carolinapecten eboreus* (Conrad, 1833). This species has a typical pectinid form
76 but reaches an unusually large size (Fig. 1A), specimens up to 165 mm in height being
77 known. Jones and Allmon (1995, fig. 10) obtained a long-wavelength ontogenetic profile of
78 $\delta^{18}\text{O}$ from a large Florida Pliocene specimen. According to the standard interpretation of
79 ontogenetic $\delta^{18}\text{O}$ profiles as signatures of seasonal temperature change, such long wavelength
80 implies very rapid growth, which might have been a product of the high primary production
81 indicated by other evidence (Allmon 1993; Allmon et al., 1995, 1996). We evaluate this
82 possibility, and the question of whether decline in food supply rather than temperature led to
83 the extinction of *C. eboreus*, through a wider investigation of growth rate in the species under
84 circumstances of differing production and temperature. We use the associated fauna as an
85 indicator of production and supply new estimates of temperature from shell $\delta^{18}\text{O}$, also
86 employing the seasonal fluctuation in this parameter as a time-marker to determine growth
87 rate. We use shell $\delta^{13}\text{C}$ and the number and size of microgrowth increments (Fig. 1E, 1F) as
88 supplementary indicators of production and growth rate, respectively.

89 Nearly 250 bivalve species were lost during the Plio-Pleistocene on the US eastern
90 seaboard (Stanley 1986), so our results from one can only hint at the factor(s) affecting the
91 rest. We hope, however, that our findings stimulate research on other species, and that the
92 methodology we adopt (an application of sclerochronology) is seen as an approach worth
93 repeating. Determining the cause of this recent mass extinction event is a worthwhile
94 objective because of the potential for insights into the cause of other such events in the more
95 distant past, and into the likely response of the current biota to environmental changes in the
96 near future (e.g., global warming; Saupe et al. 2014a, b).

97

98 SCALLOP MODE OF LIFE, GROWTH RATE AND ENVIRONMENT:

99 A FRAMEWORK FOR INVESTIGATING EXTINCTION

100

101 Most bivalves are suspension feeders and are benefited by morphological adaptations
102 and/or life positions that confer stability, hence enabling uninterrupted acquisition of the
103 small food particles concerned. A few scallops cement but most obtain stability by byssal
104 attachment at small to medium sizes. Species growing to more than about 50 mm in height
105 progressively abandon byssal attachment and become recliners (Brand 1991), obtaining
106 stability through the weight of the shell. Additional thickening would be beneficial in this
107 context, as well as a defence against crushing, drilling and prying predators, and has been
108 used by a few forms (e.g., *Fortipecten*: Hayami and Hosoda 1988; Nakashima et al. 2004).
109 However, the supplementary weight interferes with the alternative strategy towards predators
110 available to scallops: escape through swimming. In many species, shell strength is increased
111 without much addition of weight by plication (corrugation), thus preserving swimming ability
112 to larger sizes. However, above about 70 mm, even the small weight increase associated with
113 plication appears to be too much to permit swimming—at any rate, plicate scallops rarely
114 swim above this size (e.g., Jenkins et al. 2003). By contrast, the non-plicate scallop
115 *Placopecten* swims to a height of 100 mm (Dadswell and Weihs 1990), when differential
116 increase in shell weight relative to the ability to provide forward propulsion and lift makes
117 swimming mechanically impossible (Gould 1971). Beyond the height at which they are able
118 to swim, scallops must adopt a ‘siege’ rather than ‘flight’ strategy towards predators, making
119 use of the resistance to breakage, penetration and manipulation conferred by ontogenetic
120 increase in shell thickness and by large size itself (Harper and Skelton 1993; Arsenault and
121 Himmelman 1996; Harper et al. 2009). Numerous scallop species grow to a height at which
122 they are immobile recliners so it would seem that a siege strategy towards predators is
123 superior to flight (confirmed for *C. eboreus* by the absence of mollusk drillholes in the very
124 many Plio-Pleistocene individuals above 80 mm height held by the Florida Museum of

125 Natural History, but presence in smaller scallops; Harper 2002; A.L.A. Johnson, personal
126 observation, 2015). The rapid growth of many scallops (Bricelj and Shumway 1991, fig. 7)
127 makes a siege strategy effective relatively early in life, and it is reasonable to surmise that
128 any environmental circumstances favoring unusually rapid growth would be exploited for the
129 benefits in relation to predation. Of the various factors affecting growth in bivalves,
130 temperature and food supply are the most important in shelf settings of normal marine
131 salinity, both in the group generally (Johnson et al. 2007; Moss et al. 2016, 2017; Abele et al.
132 2017) and scallops specifically (Bricelj and Shumway 1991; Thompson and Macdonald
133 1991). Evidence of unusually rapid growth can therefore be taken as a probable indication of
134 relatively high temperature or primary production (the ultimate regulator of food supply to
135 suspension-feeding bivalves, whether the particles ingested are living phytoplankton or
136 organic detritus). Where one of these explanations is indicated independently, it can be
137 presumed to be the cause of rapid growth.

138 In subsequent sections we describe temperature and primary production, as currently
139 understood, in six time-space divisions of the Plio-Pleistocene sequence of the US eastern
140 seaboard, predict variation in bivalve growth-rate amongst these divisions for models of
141 temperature- and production-controlled growth, and then compare growth-rate results from *C.*
142 *eboreus* with the predictions of each model. The environmental information supplied
143 alongside growth-rate evidence by isotopic data from *C. eboreus* provides a significantly
144 altered picture of temperature differences, and a slightly altered one of production
145 differences, between the time-space divisions.

146

147 *CAROLINAPECTEN EBOREUS*: BACKGROUND INFORMATION

148 AND MATERIAL INVESTIGATED

149

150 Forms that the authors of earlier systematic studies (Waller 1969; Gibson 1987) had
151 referred to *Argopecten eboreus* (Conrad) were placed in the new genus *Carolinapecten* by
152 Ward and Blackwelder (1987). The latter authors recognised only the species *C. eboreus*, but
153 some authors (e.g., Petuch and Roberts 2007; Ward 2008; Waller 2018) have recognised
154 others, although these species (like the various subspecies that have been recognised; Gibson
155 1987; Campbell 1993; Waller 2018) can be conceived as part of a single evolving lineage.
156 This lineage, for which the name *C. eboreus* is used herein, arose in the Miocene and became
157 extinct in the Pleistocene, having undergone little net phyletic change. Waller (1969) classed
158 *C. eboreus* as an open-marine form. Other members of the *Argopecten gibbus* stock, from
159 which he considered it to have evolved, were classed as bay scallops—i.e., inhabitants of
160 semi-enclosed areas of sea, subject to fluctuations in salinity through fluvial discharge or
161 evaporation.

162 The isotopic data from the Florida Pliocene *C. eboreus* specimen studied by Jones and
163 Allmon (1995) was supplemented by Krantz (1990), who supplied $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ profiles
164 from 12 Pliocene and Pleistocene *C. eboreus* specimens from Virginia and North Carolina.
165 We have used these authors' isotopic results alongside our own (from 19 further specimens)
166 to derive the fullest possible picture of variation in growth rate in relation to environment.
167 Our strategy was to obtain an overview for the later part of the temporal range of *C. eboreus*,
168 i.e., leading up to its extinction. We therefore ignored Miocene specimens and investigated
169 individuals representing three broad time-intervals—'early Pliocene' (EPLI; essentially
170 Zanclean: 5.3–3.6 Ma), 'late Pliocene' (LPLI; essentially Piacenzian: 3.6–2.6 Ma) and early
171 Pleistocene (EPLE; Gelasian and Calabrian: 2.6–1.8 Ma)—from each of the Middle Atlantic
172 Coastal Plain (MACP) and Gulf Coastal Plain (GCP). The data is weighted towards the LPLI
173 and EPLE intervals (14 specimens from each) and includes some from the youngest
174 formation containing *C. eboreus* in the GCP (Bermont Formation; Calabrian). At the time of

175 data acquisition we thought that this was the youngest unit containing *C. eboreus* anywhere.
176 However, we later discovered that the species occurs in the Flanner Beach and Canepatch
177 formations of the MACP (Ward 2008), which are either of equivalent age to the Belmont
178 Formation (Petuch and Roberts 2007) or from the middle Pleistocene (Ionian/Chibanian): ~
179 0.5 Ma (Whitehead 1983; Ward 2008) or ~ 0.2 Ma (Miller 1985).

180 Note that we follow the recent revision of the geologic time scale (Gibbard et al. 2010),
181 such that the Pliocene-Pleistocene boundary is at 2.6 Ma, with the Gelasian (formerly late
182 Pliocene) now being the first stage in the Pleistocene. The ‘mid-Pliocene’ of previous authors
183 (e.g., Dowsett et al. 2009; Williams et al. 2009; Winkelstern et al., 2103; Johnson et al. 2017)
184 falls within the late Pliocene as defined above.

185 The specimens isotopically sampled by ourselves were either collected for the study
186 (accessioned at the University of Derby: UD), or made available from existing collections at
187 the Virginia Museum of Natural History (VMNH) and Florida Museum of Natural History
188 (UF). To convey their time-space division, both the specimens sampled by ourselves and
189 those sampled by Krantz (1990) and Jones and Allmon (1995) have been assigned new
190 reference codes incorporating this information (Fig. 2). The specimens derive from the
191 following units and locations (Fig. 3): EPLI-MACP—lower Yorktown Formation (Sunken
192 Meadow Member) at Lee Creek Mine, Aurora, North Carolina (EPLI-MACP 1) and
193 Claremont, Virginia (EPLI-MACP 2); EPLI-GCP—Unit 11 (Petuch 1982) at Sarasota, west-
194 central Florida (EPLI-GCP 1, 2); LPLI-MACP—upper Yorktown Formation (Rushmere,
195 Morgarts Beach and Moore House members) at Lee Creek Mine, Aurora, North Carolina and
196 near/at Suffolk, Petersburg and Deep Creek, Virginia (respectively, LPLI-MACP 1, 2–6, 7,
197 8); LPLI-GCP—Tamiami Formation/Pinecrest Beds, Unit 2–10 (Petuch 1982), Sarasota
198 County, west-central Florida (LPLI-GCP 1, 2, 4–6) and Jackson Bluff Formation, Leon
199 County, north Florida (LPLI-GCP 3); EPLE-MACP—Chowan River Formation at Colerain

200 Beach, North Carolina (EPLE-MACP 1–7) and Deep Creek, Virginia (EPLE-MACP 8–10),
201 and James City Formation at Lee Creek Mine, Aurora, North Carolina (EPLE-MACP 11, 12);
202 EPLE-GCP—Caloosahatchee or Bermont Formation, Charlotte County, west-central Florida
203 (EPLE-GCP 1) and Bermont Formation, Hillsborough County, west-central Florida (EPLE-
204 GCP 2). More precise stratigraphic information (where available) is provided in
205 Supplementary Data File 1, together with evidence of age. Despite uncertainties, possible
206 ages show little overlap between specimens taken to represent different time intervals (EPLI,
207 LPLI or EPLE; Fig. 2).

208

209 GROWTH-RATE PREDICTIONS FROM EXISTING EVIDENCE OF ENVIRONMENT

210

211 Extensive use has been made of biotic assemblages to interpret temperature and primary
212 production in the Plio-Pleistocene of the US eastern seaboard, and substantial variation in
213 both parameters has been recognised over the time-space divisions identified above (e.g.,
214 Hazel 1971, 1988; Ward et al. 1991; Cronin and Dowsett 1996; Allmon 1993, 2001; Allmon
215 et al. 1995, 1996). Geochemical (mainly isotopic) approaches have added considerably to
216 understanding of temperature variation (e.g., Krantz 1990; Roulier and Quin 1995; Jones and
217 Allmon 1995; Goewert and Surge 2008; Tao and Grossman 2010; Winkelstern et al. 2013;
218 Brachert et al., 2014; Johnson et al. 2017) but so far have only been used a little to investigate
219 production (Krantz 1990; Jones and Allmon 1995; Tao and Grossman 2010), with a focus on
220 determining the cause of variation. In the next sections, we use existing isotopic ($\delta^{18}\text{O}$)
221 temperature data from mollusks (where available) in combination with qualitative
222 assessments of production from faunal composition to characterise the environment of each
223 division. We thus identify which divisions should yield evidence of rapid growth if
224 temperature or production was the controlling factor. Isotopic temperature data of a similar

225 (seasonal) resolution to that from mollusks has been obtained from corals (e.g., Roulier and
226 Quinn 1995) but there are discrepancies between the two datasets—e.g., systematically lower
227 seasonal temperature variation indicated by corals (Brachert et al. 2014). Combining the
228 datasets would have obscured differences between the divisions.

229

230

Temperature

231

232 With the exception of information from the lower James City Formation of the early
233 Pleistocene (Krantz 1990), Johnson et al. (2017) summarised all the available molluscan $\delta^{18}\text{O}$
234 data (entirely from bivalves) for the early Pliocene to early Pleistocene of the MACP, giving
235 temperatures calculated for appropriate values of water $\delta^{18}\text{O}$. Winter minimum and summer
236 maximum temperatures for specific units and taxa (including already-analysed
237 *Carolinapecten*) are listed in Table 1. Temperatures for the lower James City Formation,
238 calculated on the same basis as those for the early Pleistocene Chowan River Formation (i.e.,
239 water $\delta^{18}\text{O} = 0.00\text{‰}$) have been added. Table 1 shows that material of LPLI age gives higher
240 winter and summer temperatures than material of EPLI and EPLE age. We can conveniently
241 define high temperature conditions (represented by LPLI data) and differentiate these from
242 low temperature conditions (represented by EPLI and EPLE data) by setting winter and
243 summer boundaries of 11.5 °C and 24 °C, respectively, between the two.

244

245 Applying the classification scheme adopted for the MACP to the GCP, gastropod-derived
246 data from Unit 7 of the Pinecrest Beds (LPLI) clearly falls within the high temperature
247 category: mean winter and summer isotopic temperatures calculated using an appropriate
248 value (+1.02‰) for water $\delta^{18}\text{O}$ are 18 and 27 °C, respectively (Tao and Grossman 2010, table
249 1). On the basis of Sr/Ca data, Tao and Grossman (2010) argued that their lower gastropod-
derived isotopic temperatures from Unit 4 (also LPLI) reflected inappropriate use of the same

250 value for water $\delta^{18}\text{O}$. A higher value (reflecting likely evaporative enrichment of ^{18}O in
251 seawater during deposition of this unit) would have yielded correspondingly higher
252 temperatures. Earlier gastropod and bivalve $\delta^{18}\text{O}$ data from other LPLI (and EPLE) units
253 within the Pinecrest Beds (Jones and Allmon 1995) yields temperatures generally similar to
254 the more recent gastropod data from Unit 7 when calculated using a water $\delta^{18}\text{O}$ of +1.02‰
255 (Tao and Grossman 2010, figure 4). Use of this value for gastropod $\delta^{18}\text{O}$ data from the
256 Caloosahatchee Formation (EPLI) yields mean winter and summer temperatures of 17 and
257 27 °C, respectively (Tao and Grossman 2010, table 1). However, we prefer (see below) a
258 value of 0.00‰ for the EPLE interval, which yields temperatures 4–5 °C lower, within the
259 high temperature category as defined above for winter but outside it for summer. We
260 therefore recognise an additional low summer (LS; < 24 °C)/high winter (HW; \geq 11.5 °C)
261 temperature category. This category appears to be represented not only by the EPLE-GCP but
262 also the EPLI-GCP division. No isotopic temperature data has been provided hitherto for the
263 latter but ostracod-assemblage analysis gives mean winter and summer temperatures (16 and
264 22 °C, respectively; Cronin and Dowsett 1996) that fall within the LS/HW category. Isotopic
265 evidence from the MACP indicates that ostracod-assemblage analysis may yield winter
266 temperatures that are overestimated by 3–4 °C (Johnson et al. 2017). However, subtraction of
267 this amount from the assemblage-derived EPLI-GCP winter value still leaves a figure in the
268 high temperature range. In view of the refinement to the classification scheme necessitated by
269 EPLI-GCP and EPLE-GCP data it is appropriate also to recognise a high summer (HS; \geq 24
270 °C)/low winter (LW; < 11.5 °C) temperature category, not represented by existing data from
271 the early Pliocene to early Pleistocene of the US eastern seaboard, but into which new data
272 might fall.

273

274

Primary production

275

276 The Miocene of the US eastern seaboard is characterised by thick phosphorite deposits,
277 almost certainly reflecting high primary production, i.e., a supply of organic material too
278 large for respiration to prevent its accumulation on the seafloor (Riggs 1984; Riggs et al.
279 2000; Snyder et al. 1990). Phosphate is also present in many Pliocene and early Pleistocene
280 units, and occurs in amounts up to 25% in the EPLI interval (Riggs et al., 1982), but was
281 probably derived from erosion of Miocene phosphorites rather than generated
282 contemporaneously (Riggs et al. 2000; S.R. Riggs, personal communication, 2016).
283 Nevertheless, compelling evidence of high production exists for some Pliocene units in the
284 form of rich marine vertebrate faunas, including numerous fish-eating birds and other
285 predators, some of large size. The occurrence of common turrilline gastropods has been
286 used as an indication of high production (e.g., Allmon 2011; Allmon et al. 1995; Anderson et
287 al. 2017). However, in some situations high frequencies reflect cool water rather than high
288 production (Allmon and Dockery 1992) so to avoid ambiguity we limit the following
289 discussion to vertebrate evidence. Existing geochemical evidence of production is too scant
290 to permit comparison between divisions by this means.

291 The Pliocene Yorktown Formation of Lee Creek Mine, Aurora, North Carolina, has
292 yielded an abundant and diverse fauna of marine fish (Fierstine 2001; Purdy et al. 2001),
293 including the giant shark *Carcharocles megalodon*, together with diverse, sometimes large,
294 carnivorous marine mammals (Kohno and Ray 2008; Koretsky and Ray 2008; Whitmore and
295 Barnes 2008; Whitmore and Kaltenbach 2008; Kazár and Bohaska 2008), and an abundant
296 avifauna consisting of over 100 species, mostly marine fish-eating forms (Olson and
297 Rasmussen, 2001; Storer 2001; Olson and Hearty 2003). Virtually all the many thousands of
298 vertebrate specimens are from spoil but characteristics of the attached matrix allowed the
299 above authors to assign much of the material to the lower part of the formation, i.e., the

300 Sunken Meadow Member (EPLI-MACP). While noting that some vertebrate material is from
301 higher horizons (thus ruling out exceptional preservational circumstances in the lower
302 Yorktown Formation), Ward (2008) agreed that most came from the Sunken Meadow
303 Member, remarking (p. 360) in a summary of the biota of the overlying Rushmere and
304 Morgarts Beach members (LPLI-MACP) that the ‘relative lack of vertebrates is especially
305 noticeable.’ The same pattern is evident elsewhere in the MACP. For instance, Kohno and
306 Ray (2008) list numerous EPLI occurrences of walrus but just one definite LPLI record
307 (Appendix II, number 4; a locality in Virginia exposing only the upper Yorktown Formation
308 according to Ward and Blackwelder 1980); similarly, there is just a single LPLI record of a
309 whale and of a seal, both from Rice’s Pit, Hampton, Virginia (Westgate and Whitmore 2002;
310 Koretsky and Ray 2008, p. 114). Ward (2008) recorded no vertebrates at all from the
311 uppermost (Moore House) member of the Yorktown Formation or from the early Pleistocene
312 Chowan River Formation at Lee Creek, but a walrus femur from Yadkin Pit, Deep Creek,
313 Virginia, may be from the latter unit, even if probably reworked from the Yorktown
314 Formation (Kohno and Ray 2008, Appendix 1; Appendix 2, number 5). The depauperate
315 nature of the EPLE-MACP vertebrate fauna is also evident in the younger James City
316 Formation at Lee Creek, from which Ward (2008) listed only a restricted fish assemblage
317 (four species), commenting (p. 384) that the ‘scarcity of shark, ray and bony fish remains in
318 units above the Sunken Meadow Member of the Yorktown Formation (lower Pliocene) is
319 reflected in all of the stratigraphic units along the Atlantic Coastal Plain. The James City
320 Formation is typical in this regard.’ Certainly the still younger Flanner Beach Formation is no
321 exception: Ward (2008) lists no vertebrates from this at Lee Creek.

322 On the basis of the abundance, diversity and ecology of vertebrates from Lee Creek, Olson
323 and Rasmussen (2001, p. 238) opined: ‘The Yorktown seas off present-day North Carolina
324 must have supported one of the greatest levels of marine productivity in the history of the

325 earth.’ In that most of the Yorktown marine vertebrate fauna (here and elsewhere in the
326 MACP) is from the Sunken Meadow Member, this statement can be taken to apply to the
327 EPLI interval, with much lower production in the LPLI and EPLE intervals in the MACP,
328 probably at something like the ‘average’ shelf level characteristic of the US eastern seaboard
329 at present (FAO 1981, map 1.1).

330 While it lacks birds and has a fish fauna apparently limited to sharks (Petuch and Roberts
331 2007), the vertebrate fauna of Unit 1 of the Sarasota, Florida, sequence (EPLI-GCP) includes
332 abundant and diverse carnivorous marine mammals, some of large size (Emslie and Morgan
333 1994; Allmon et al. 1996), and thus resembles that of the Sunken Meadow Member.
334 Similarly high production can therefore be inferred. Unlike in the MACP, high production
335 evidently continued (or at least recurred) in the LPLI interval in the GCP. A bed at the
336 Richardson Road Shell Mine (= Quality Aggregates pit), Sarasota, that is contemporaneous
337 with or somewhat older than Unit 4 (Allmon 1993), contains an avifauna of 11 taxa, with one
338 extinct, probably marine, cormorant species represented by 137 skeletons and thousands of
339 separate bones (Emslie and Morgan 1994; Emslie et al. 1996). No fully marine cormorants
340 live in Florida now so the occurrence of such a form in large numbers during the LPLI
341 interval provides good evidence of more abundant food than at present in the shape of marine
342 fish, and thus of higher primary production (Allmon et al. 1996). By the EPLE interval
343 production had seemingly declined in the GCP to something like the present ‘average’ level
344 (FAO 1981, map 1.1): two seabird species (an alcid and an albatross; both known from single
345 bones) are recorded from the Caloosahatchee Formation and a seal from the Bermont
346 Formation, suggesting a fairly limited marine bird and mammal fauna, similar to that at
347 present in Florida and contrasting sharply with the Pliocene (Allmon et al. 1996).

348

349

Growth-rate predictions

350

351 On the basis of present evidence, nearly all possible combinations of the temperature and
352 production categories identified above are represented by time-space divisions in the Plio-
353 Pleistocene of the US eastern seaboard (Fig. 4). We can expect there to have been a
354 temperature and level of production above which growth in *C. eboreus* was inhibited rather
355 than promoted. Tests of the influence of each parameter on growth are therefore best framed
356 in terms of predictions relating to relatively low values of each. Thus if temperature was the
357 control we should not expect to see rapid growth in settings of low winter and summer
358 temperature (in the EPLI-MACP and EPLE-MACP divisions from present evidence); if
359 production was the control we should not expect to see rapid growth in settings of ‘average’
360 production (in the LPLI-MACP, EPLE-MACP and EPLE-GCP divisions from present
361 evidence); and if both were involved we should not expect to see rapid growth in settings of
362 low winter and summer temperature combined with ‘average’ production (in the EPLE-
363 MACP division from present evidence).

364

365 LABORATORY METHODS AND TREATMENT OF DATA

366

367 As indicated above, we used the isotopic data of Krantz (1990) and Jones and Allmon
368 (1995) to supplement our own from *C. eboreus*. The specimen investigated by Jones and
369 Allmon (1995) was available, so we obtained complementary microgrowth-increment data
370 from it. The specimens analysed by us were (where necessary) initially scrubbed with a nylon
371 brush in tap-water to remove loosely adherent sediment. They were then coated with a
372 sublimate of NH₄Cl and digitally photographed. Images were inserted into the bespoke
373 software Panopea© (2004, Peinl and Schöne) for counting and measurement of microgrowth
374 increments, together with measurement of the position of significant growth breaks,

375 subdivided into major and moderate according to the size of the ‘step’ in the shell profile
376 (Fig. 1A, 1C, 1F). In all shells the lamellae bounding microgrowth increments had been
377 affected by abrasion near the dorsal margin (umbonal area), preventing acquisition of
378 complete microgrowth-increment records, and visibility was sometimes poor elsewhere.
379 Measurements of increment sizes and growth-break positions were made principally along
380 the mid-line (axis of maximum growth = anatomical height) but for most shells it was
381 preferable (e.g., to avoid areas of abrasion), and for two broken shells (e.g., Fig. 1C)
382 necessary, to include measurements taken somewhat anterior or posterior of this line. In such
383 instances increment sizes and growth-break ‘heights’ were mathematically adjusted
384 (multiplied by umbo–margin distance along mid-line/umbo–margin distance through
385 measurement position) to correspond to measurements along the mid-line. The same
386 adjustment was made to the measured position of isotope samples where these were taken
387 away from the mid-line—e.g., in cases of breakage or other shell imperfections (see below).

388 Following removal of the NH_4Cl coating by washing in tap-water, specimens for isotopic
389 analysis were thoroughly cleaned using the method adopted by Valentine et al. (2011).
390 Samples were extracted by drilling successive, continuous or discontinuous (plical crests
391 only) grooves up to about 1 mm deep in the outer shell layer (foliated calcite apart from a
392 short prismatic-calcite stage in the right valve; Waller 1978), using a hand-held drill equipped
393 with a 0.5 mm bit. The spacing of grooves was varied according to microgrowth-increment
394 size (and hence presumed growth rate) to achieve roughly comparable temporal resolution
395 within and between specimens: mean spacings for individuals (as determined for the axis of
396 maximum growth) are 1.5–4.7 mm. Cracks and areas significantly abraded or with a high
397 concentration of microborings were avoided. In a few instances, encrusting organisms or
398 sediment were drilled away to reveal the shell; the outermost part of the shell itself (~ 0.1
399 mm) was also drilled away in a few cases where it had an unusual colour or texture. Where

400 practicable, sampling was started very close to the dorsal margin (origin of growth) and
401 continued to the ventral margin, but in some cases breakage or abrasion had reduced the
402 already small amount of material recoverable close to the dorsal margin to such an extent that
403 sampling had to commence more ventrally. It was noted in sampling close to the dorsal
404 margin that material of a different (often 'crystalline') character to that of the (there thin)
405 outer shell layer was sometimes revealed and possibly included in the material extracted.
406 Samples were removed from the site of extraction by partially or wholly inverting the shell
407 such that, with the assistance of tapping or brushing, the powder fell onto a slip of aluminium
408 foil for collection and transfer into a non-stick storage vial. After extraction and removal of
409 each sample the shell was thoroughly brushed to prevent contamination of the next sample.

410 Measurement of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ was carried out either at the NERC Isotope Geosciences
411 Laboratory, British Geological Survey, Keyworth, UK, or at the Institute of Geosciences,
412 University of Mainz, Germany. Analysis at Keyworth involved an Isoprime dual inlet mass
413 spectrometer coupled to a Multiprep system; powder samples were dissolved with
414 concentrated phosphoric acid in borosilicate Wheaton vials at 90 °C. Analysis at Mainz
415 involved a Thermo Finnigan MAT 253 continuous flow-isotope ratio mass spectrometer
416 coupled to a Gasbench II; powder samples were dissolved with water-free phosphoric acid in
417 helium-flushed borosilicate exetainers at 72 °C. Both laboratories calculated $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$
418 against VPDB and calibrated data against NBS-19 and their own Carrara Marble standard;
419 values were consistently within $\pm 0.05\text{‰}$ of the preferred values for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in NBS-
420 19. For a few shells, part of the sample series was analysed in one laboratory and part in the
421 other; there was found to be excellent agreement (e.g., smooth continuation of trends)
422 between the subsets of data. Reproducibility was checked by remeasuring some samples, and
423 in the case of seemingly aberrant initial results, repeat sampling and analysis was undertaken
424 (both initial and replicate values are plotted in Figs. 5–8). Results from repeat sampling were

425 nearly always closer to expectation (implying some contamination of the initial samples) and
426 in such cases were used with singleton values from other positions to generate ontogenetic
427 profiles (lines in Figs. 5–8). Otherwise, the profiles connect singleton values with mean
428 values from multiple sampling (and multiple measurement). Figure 6A contains the isotopic
429 results of Jones and Allmon (1995; read off from fig. 10).

430 To conform with recent work on Plio-Pleistocene scallops from the US eastern seaboard
431 (Johnson et al., 2017), temperatures were derived from shell $\delta^{18}\text{O}$ using the calcite equation
432 (1) of Epstein et al. (1953):

433

$$434 \quad T = 16.5 - 4.3(\delta^{18}\text{O}_{\text{calcite}} - \delta^{18}\text{O}_{\text{seawater}}) + 0.14(\delta^{18}\text{O}_{\text{calcite}} - \delta^{18}\text{O}_{\text{seawater}})^2 \quad (1)$$

435

436 We subtracted 0.27‰ from our $\delta^{18}\text{O}$ water values (calibrated against SMOW) in order to
437 adjust them to the VPDB scale used for shell carbonate (Gonfiantini et al. 1995). Various
438 initial values for water $\delta^{18}\text{O}$ were used. Whilst noting that global, negative estimates have
439 been adopted by some workers (discussed in Johnson et al. 2017), we favor the model-based,
440 regional, positive estimates for the Pliocene given by Williams et al. (2009): +0.70 and
441 +0.90‰ for the early Pliocene of the MACP and GCP, respectively; +1.10 and +1.02‰ for
442 the late Pliocene of the MACP and GCP, respectively. We calculated temperatures from each
443 Pliocene $\delta^{18}\text{O}$ profile using all four estimates of water $\delta^{18}\text{O}$ but prefer those based on the
444 relevant division-specific value. Model-based regional estimates of water $\delta^{18}\text{O}$ do not exist
445 for the early Pleistocene of the US eastern seaboard so we used the set of four estimates (–
446 0.20, 0.00, +0.20, +0.50‰) employed by Winkelstern et al. (2013) for this interval, following
447 these authors in adopting 0.00‰ as the preferred value.

448 Notwithstanding the existence of some ‘noise’, the summer (low values) and winter (high
449 values) parts of $\delta^{18}\text{O}$ profiles were in general readily identifiable (problematic cases are

450 discussed in the next section). In accordance with the approach of Johnson et al. (2017), we
451 used the maxima and minima of unsmoothed profiles to derive values for extreme winter and
452 summer temperatures. The shell heights of maxima and minima were likewise used to
453 determine the size of half- and (in most cases) whole-year shell increments—i.e., growth rate.
454 As for estimation of seasonal temperature, the use of maxima and minima from unsmoothed
455 $\delta^{18}\text{O}$ profiles to determine the size of half- and whole-year increments introduces the
456 possibility of error relating to noise. However, smoothing has some disadvantages (e.g.,
457 amplification of the effect of growth breaks; Johnson et al. 2017) and is not a solution to
458 errors of a more systematic nature (see discussion of early ontogenetic excursions below). As
459 will be shown, *C. eboreus* had a very short lifespan (never exceeding two years and rarely
460 much more than one) so only a modest proportion of the $\delta^{18}\text{O}$ profiles (9 of 32) contain two
461 maxima and/or minima, others showing one maximum and one minimum or a single
462 maximum/minimum (partly due to incomplete or inadequate shell preservation). In cases of
463 the last two types it was only possible to obtain minimum values for whole- and half-year
464 increments, respectively. We determined the largest half- and (for individuals that lived
465 sufficiently long) whole-year increment from each profile, measuring the size of the largest
466 whole-year increment between consecutive $\delta^{18}\text{O}$ maxima or minima, or between other
467 homologous points (i.e., $\delta^{18}\text{O}$ values representing equivalent times of year) where this gave a
468 larger value. The approach is illustrated in Figures 5–8, where we have identified the points
469 on the $\delta^{18}\text{O}$ profiles between which half-year and whole-year increments were measured (see
470 also Fig. 1A–C). The same methodology was followed in measurement of increment sizes
471 from the $\delta^{18}\text{O}$ profiles of Krantz (1990). Annotated versions of these profiles are available
472 online as Supplementary Data File 2, and other raw data as Supplementary Data File 3.

473

474

RESULTS AND ANALYSIS

475

476

Oxygen Isotope Data

477

478 *Problematic Profiles.*—Most of the $\delta^{18}\text{O}$ profiles in Figures 5–8, together with those
479 obtained from *C. eboreus* by Krantz (1990), are of a form readily interpretable in terms of the
480 seasonal temperature cycle. However, a few profiles present problems. The profile from
481 EPLI-GCP 1 (Fig. 5A) shows only slight variation in $\delta^{18}\text{O}$ compared to another specimen of
482 comparable size from the same division (EPLI-GCP 2; Fig. 5C). The similar or greater $\delta^{18}\text{O}$
483 values from EPLI-GCP 1 compared to winter values from EPLI-GCP 2 suggest that the
484 former profile is a (somewhat ‘noisy’) record of winter alone, but microgrowth-increment
485 data (see below) indicates that over a year is represented. Accepting the latter evidence, we
486 have assumed that the modest reduction in $\delta^{18}\text{O}$ at approximately 45 mm shell height marks
487 the second of two summer intervals, and have determined seasonal temperatures, and half-
488 and whole-year shell increments, accordingly. The profile from LPLI-GCP 3 (Fig. 6C) shows
489 even less variation and values intermediate between the winter and summer values of shells
490 from the same division. Microgrowth-increment data indicates that this shell lived only a few
491 months, hence it is entirely plausible that only one of these seasons is represented. We have
492 assumed it to be winter because the $\delta^{18}\text{O}$ values are closer to the mean of maxima rather than
493 minima from other shells of the same division. The profile from LPLI-GCP 2 (Fig. 6B) is
494 problematic because it shows an excursion to high values (the highest in the profile) at about
495 75 mm, interrupting a smooth trend to low values. Rather than representing winter, it may be
496 that these high values reflect a downturn in temperature during spring; such fluctuations are
497 certainly evident in other profiles (e.g., at about 65 mm in LPLI-GCP 6; Fig. 6F). However,
498 for consistency with the approach applied to other profiles we have assumed that the values
499 around 75 mm are representative of winter and have determined seasonal temperatures and

500 half- and whole-year increments in accordance with this. A final problem is represented by
501 abrupt excursions to lower values in early ontogeny, in some cases to the lowest values in the
502 profiles (starred values in Figs. 6A, 6E, 7D). If these values are taken to represent summers
503 the adjacent inflections have to be interpreted as winters. However, the values involved in the
504 inflections are inconsistent with this, being much lower than clear winter values later in the
505 profiles. It seems probable that the early ontogenetic $\delta^{18}\text{O}$ excursions (which in the cases
506 highlighted are matched by excursions in $\delta^{13}\text{C}$) reflect incorporation into samples of material
507 from below the thin outer layer (see previous section). The ‘crystalline’ material seen at
508 shallow depths in the umbonal area could have been altered myostracal aragonite. If this had
509 equilibrated with groundwaters of meteoric origin (typically low $\delta^{18}\text{O}$) and been incorporated
510 into samples it would have imparted a lower $\delta^{18}\text{O}$ to them. In view of the likely diagenetic
511 origin of early ontogenetic ‘spikes’, we have disregarded them in seasonal interpretation of
512 $\delta^{18}\text{O}$ profiles and calculation of seasonal temperatures. It is worth mentioning here that there
513 is little evidence from aberrant $\delta^{18}\text{O}$ values for alteration of outer-layer calcite.

514

515 *Characteristics of Profiles.*—We here itemise the general features of profiles and their life-
516 history implications; the temperatures and specific overall growth rates implied are discussed
517 later.

518 1. Only about half the profiles in Figures 5–8 show a full seasonal cycle and just two
519 (LPLI-GCP 6, EPLE-MACP 1) show as much as 1.5 cycles. A similar proportion of the
520 profiles obtained by Krantz (1990) show a full cycle, one (EPL-MACP 4) showing about
521 1.5 cycles and another (EPL-MACP 9) about 1.75 cycles. Since the latter profile starts at a
522 shell height above 20 mm, it is conceivable that a complete ontogenetic profile would have
523 shown two full cycles. It appears therefore that *C. eboreus* lived no longer than two years, in

524 some cases (e.g., LPLI-GCP 6; height 165 mm, age 1.5 years) reaching a very large size in a
525 shorter time.

526 2. Amongst the profiles from the MACP in Figures 5, 7 and 8, all start at or somewhat
527 before a summer minimum (i.e., post-larval growth commenced in the spring or summer),
528 that from LPLI-MACP 5 starting earliest but clearly on a declining trend. While some from
529 the GCP in Figures 5, 6 and 8 start a little before (but never at) a summer minimum, the
530 profiles from EPLI-GCP 1 and 2, LPLI-GCP 6 and EPLE-GCP 2 (and probably also LPLI-
531 GCP 2 and 3) start at or somewhat before a winter maximum (i.e., in the fall or winter), that
532 from LPLI-GCP 6 starting earliest, at a value considerably less than the winter maximum.
533 The profiles provided by Krantz (1990), all from the MACP, start at a shell height of 15 mm
534 or more so it is impossible to be sure about the time of onset of growth. However, since all
535 start at low $\delta^{18}\text{O}$ values, and some show a subsequent fall, it is likely that post-larval growth
536 commenced in the spring or summer.

537 3. Only a few profiles terminate (i.e., the individual died) in summer (e.g., LPLI-GCP 2,
538 LPLI-MACP 6) and many in winter. However, of the six largest individuals (height > 120
539 mm), five died during the spring rise in temperature (LPLI-GCP 1, 5, 6; LPLI-MACP 1;
540 EPLE-GCP 1). Since these individuals were evidently not compromised by low temperatures,
541 would have been relatively immune from predation through their size (see earlier discussion),
542 and were still young, they possibly died after their first reproductive (spawning) event—i.e.,
543 *C. eboreus* may have been semelparous (Cole 1954). High winter mortality at smaller sizes
544 might reflect a cold-induced lowering of swimming capacity and consequent reduced ability
545 to escape predators by this means (see earlier discussion).

546 4. Of the profiles in Figures 5–8, only that for EPLE-MACP 1 is close to sinusoidal, all
547 but one of the rest having a low gradient (falling and rising values) for the first half to whole
548 cycle and then steepening markedly (LPLI-GCP 6 is unusual in showing a steep rise in values

549 in earliest ontogeny, succeeded by a gradual fall). Two (EPLE-MACP 4, 9) of the profiles
550 provided by Krantz (1990) are close to sinusoidal but others that span a sufficient interval
551 show the same ontogenetic increase in steepness, which indicates a decline in growth rate. It
552 is noteworthy that the more sinusoidal profiles are all ones extending well into a second year
553 and show relatively small half- and whole-year increments (Table 2). Longer life is a
554 common corollary of slower growth amongst bivalves (Moss et al. 2016).

555 5. Where profiles are distinctly non-sinusoidal, the winter sectors are typically narrower
556 (indicating slower growth) than the summer. Exceptions to this rule are specimens from the
557 GCP showing a fall or winter start to growth (e.g., EPLI-GCP 2). The broad ‘spring’ sector in
558 the profile from LPLI-MACP 5, a specimen showing an unusually early start to growth for its
559 location, suggests that it is the time of growth onset rather than geographic position that is
560 critical in determining the relative amounts of winter and summer growth over the ontogeny
561 of an individual.

562 6. The sizes (heights) of the largest half- and whole-year increments (Table 2) are
563 extremely variable: 16.0–121.7 mm for full half-years and 26.0–145.7 mm for full whole-
564 years. The minimum estimates recorded are well below the upper limits of these ranges so it
565 is unlikely that the actual increment sizes exceeded them. The largest values for half- and
566 whole-year increment size (i.e., fastest growth rates) in *C. eboreus* are 1.6 times the
567 maximum values recorded amongst all other scallop species: 75 mm for half-year increment
568 size in modern wild *Ylistrum balloti* (Williams and Dredge 1981); 90 mm for whole-year
569 increment size in modern cultured *Argopecten purpuratus* (DiSalvo et al. 1984).

570

571 Stable Carbon Isotope Data

572

573 Amongst the $\delta^{13}\text{C}$ profiles in Figures 5–8, nearly all from the larger shells (height ≥ 100
574 mm), exhibit ontogenetic trends to lower values (reaching -5.03‰ in EPLE-GCP 1),
575 superimposed on which are more or less pronounced fluctuations, paralleling those in $\delta^{18}\text{O}$
576 profiles. However, in the large shell LPLI-GCP1 there is no overall reduction in $\delta^{13}\text{C}$ and
577 downward fluctuations do not parallel $\delta^{18}\text{O}$. The last of the downward fluctuations
578 corresponds to a $\delta^{18}\text{O}$ maximum, thus conforming to the expectations of an upwelling event
579 (Jones and Allmon 1995). However, the $\delta^{18}\text{O}$ maximum is at the end of a long-term trend to
580 higher values and so is much more reasonably interpreted as the culmination of winter
581 cooling rather than incursion of cool deep-waters. Excursions to lower $\delta^{13}\text{C}$ earlier in
582 ontogeny are not mirrored by excursions to higher $\delta^{18}\text{O}$, although the trend to increasing $\delta^{18}\text{O}$
583 is slightly steepened. This may reflect slower growth, as suggested by contemporaneous
584 reductions in microgrowth-increment size.

585 In shells less than 100 mm in height, $\delta^{13}\text{C}$ generally lies between -1.00 and $+1.00\text{‰}$, in
586 some cases fluctuating in accordance with $\delta^{18}\text{O}$ (e.g., EPLI-MACP 2), in certain others
587 showing a slight ontogenetic increase (not in accordance with $\delta^{18}\text{O}$; e.g., LPLI-MACP 4), and
588 in yet others essentially ‘flat-lining’ (e.g., LPLI-GCP 4). The range of values and patterns
589 from the smaller shells is very much like that obtained by Krantz (1990) from LPLI-MACP
590 and EPLE-MACP shells up to 100 mm. As in the larger shells, there is no evidence of
591 upwelling from inverse variation in $\delta^{13}\text{C}$ relative to $\delta^{18}\text{O}$ (cf. Jones and Allmon 1995).

592 For the smaller shells represented in Figures 5–8 and the first 100 mm of ontogeny of the
593 larger shells, mean $\delta^{13}\text{C}$ ranges from -1.90 ± 0.66 ($\pm 1\sigma$) to $+0.89 \pm 0.24\text{‰}$ (EPLI-GCP 1
594 and LPLI-MACP 4, respectively). Grand means from these shells for each of the time-space
595 divisions are as follows: EPLI-GCP: $+0.08 \pm 0.08\text{‰}$; EPLI-MACP: $-0.26 \pm 0.22\text{‰}$; LPLI-
596 GCP: $-0.11 \pm 0.69\text{‰}$; LPLI-MACP: $+0.49 \pm 0.32\text{‰}$; EPLE-GCP: $-1.36 \pm 0.54\text{‰}$; EPLE-
597 MACP: $-0.14 \pm 0.09\text{‰}$. The EPLI-GCP, EPLI-MACP and LPLI-GCP values are

598 substantially lower than the individual averages from two modern specimens of the scallop
599 *Placopecten magellanicus* from the Middle Atlantic Bight, and also lower than the individual
600 averages from two of three modern specimens of the scallop *Argopecten gibbus* from the
601 South Atlantic Bight (Krantz et al. 1988). This is consistent with the high primary production
602 inferred for these divisions, since, whether the necessary nutrients were derived by upwelling
603 or fluvial supply, they would have been associated with dissolved carbon of low $\delta^{13}\text{C}$. The
604 higher LPLI-MACP grand mean is correspondingly consistent with the ‘average’ production
605 inferred for this division. The negative EPLE-MACP value is not consistent with the
606 ‘average’ production inferred but is evidently a reflection of small sample size: nearly all the
607 individual averages of the EPLE-MACP specimens analysed by Krantz (1990) are positive.
608 Small sample size may likewise account for the negative EPLE-GCP grand mean, but the
609 value is so low that it brings into question the ‘average’ production inferred.

610 In conclusion, the $\delta^{13}\text{C}$ data provides scant evidence of short-term upwelling events, but in
611 the low individual averages contributing to low grand means they may evince more
612 protracted supply of nutrient-rich waters capable of supporting high production. Ontogenetic
613 fluctuations in $\delta^{13}\text{C}$ paralleling $\delta^{18}\text{O}$ probably reflect the interaction between seasonal cycles
614 of phytoplankton production and water-column stratification in a mid- to outer-shelf setting
615 (Arthur et al. 1983; Johnson et al. 2017; Vignols et al. 2018).

616

617 Microgrowth Increments

618

619 Microgrowth-increment profiles are only available for the specimens in Figures 5–8.
620 Despite high frequency, relatively low amplitude variation, most profiles that are sufficiently
621 long show a major (high amplitude) cycle of size change—from small to large to small—
622 within the height interval of the first $\delta^{18}\text{O}$ cycle, with increments remaining small thereafter.

623 The microgrowth-increment cycle commonly occupies substantially less than the height
624 interval of the first $\delta^{18}\text{O}$ cycle (which may be incomplete), such that the cycles are out of
625 phase. At least for the LPLI interval, for which the most data is available, this pattern is
626 evident in shells from both the MACP (e.g., LPLI-MACP 2 and 4) and GCP (e.g., LPLI-GCP
627 6). Maximum microgrowth-increment size typically corresponds to low or rising $\delta^{18}\text{O}$ in
628 shells from the MACP and high or falling $\delta^{18}\text{O}$ in shells from the GCP. However, this is
629 clearly not a reflection of geographic differences in the time of optimum growth conditions
630 but rather of the onset of growth (see above), because most exceptions to the pattern show
631 unusually early (LPLI-MACP 5) or late (LPLI-GCP 5, EPLE-GCP 1) starts to growth for
632 their respective areas. Short-term increases and decreases in increment size are matched by
633 increases and decreases in $\delta^{13}\text{C}$ in some shells (e.g. LPLI-GCP 1, LPLI-MACP 5, EPLE-GCP
634 1) but not by any notable changes (increases or decreases) in $\delta^{18}\text{O}$ over the same height
635 interval. They therefore do not relate to temperature. The correlation with $\delta^{13}\text{C}$ over short
636 intervals may manifest the same process as the mutual declines in microgrowth-increment
637 size and $\delta^{13}\text{C}$ over the course of ontogeny. This could be greater incorporation of isotopically
638 light respiratory carbon when growth rate is low, as represented by smaller microgrowth
639 increments (Lorrain et al. 2004).

640 The data for microgrowth-increment size and number confirms that the half- and whole-
641 year increments determined from $\delta^{18}\text{O}$ profiles do indeed represent time-intervals of these
642 lengths—i.e., that shell $\delta^{18}\text{O}$ reflects seasonal temperature variation rather than extreme (and
643 improbable) variation in water $\delta^{18}\text{O}$, over some unknown timescale. The major cycle of size
644 change within the first $\delta^{18}\text{O}$ cycle is very comparable with the pattern in young, cultured
645 examples of the living scallops *Aequipecten opercularis* and *Pecten maximus* (Broom and
646 Mason 1978; Owen et al. 2002). In these, microgrowth-increment size increases from late
647 winter to reach a summer maximum and then falls to a late fall minimum, succeeded by

648 several months of little or no growth. Over the period in which the largest increments are
649 formed, which is also the time of most rapid overall growth, the number laid down closely
650 corresponds to the number of days elapsed (i.e., the microgrowth increments are ‘daily’), as
651 in some other scallop species (e.g., Joll 1988; Clark 2005; Velarde et al. 2015). Outside this
652 period, fewer are laid down, such that there is an increasing discrepancy with the number of
653 days elapsed as the time-interval expands. In *C. eboreus*, increment numbers in relation to
654 $\delta^{18}\text{O}$ -defined time intervals (Table 2) exhibit similar features. The maximum number in a
655 half-year interval (208; LPLI-GCP 5) slightly exceeds the number of days (183), but this
656 could reflect inaccurate location of the summer $\delta^{18}\text{O}$ minimum: the summer sector of the
657 profile concerned (Fig. 6E) is very broad and exhibits a little ‘noise’, making it possible that
658 the position of the $\delta^{18}\text{O}$ minimum does not exactly correspond to the time of maximum
659 temperature. The next highest count (164; LPLI-GCP 6) is from the specimen exhibiting the
660 largest half-year increment (i.e., sustained rapid growth), with two other counts above 150.
661 By contrast, while all whole-year counts are less than the number of days (365), the highest
662 number is 247 (from a rapid grower; LPLI-GCP 5), representing a greater discrepancy with
663 the number of days than the four highest half-year counts. As well as confirming the annual
664 timescale of $\delta^{18}\text{O}$ cycles in *C. eboreus*, increment counts confirm the interpretations applied
665 to problematic $\delta^{18}\text{O}$ profiles showing little or no cyclicity. The half- and whole-year
666 increments recognised in EPLI-GCP 1 include 153 and 187 microgrowth increments,
667 respectively. These counts are within the ranges set by other specimens showing more
668 pronounced variation in $\delta^{18}\text{O}$. Interpreting the entire $\delta^{18}\text{O}$ profile as a record from a single
669 winter is inconsistent with the total increment count of 264, a number in excess of even the
670 whole-year maximum in other specimens. The ‘flat’ $\delta^{18}\text{O}$ profile of LPLI-GCP 3 corresponds
671 to 61 increments, a number consistent with its interpretation as a record from a single winter.

672 In some *C. eboreus* specimens, the absolute size of microgrowth increments is like that
673 typical of scallop species (Fig. 1F, 1G) but in the majority it is substantially larger (Fig. 1E;
674 Table 2). Discounting the highest mean values for half- and whole-year intervals (based on a
675 small dataset from EPLI-MACP 1, in which microgrowth increments were difficult to
676 measure), the next highest values—0.926 mm (LPLI-GCP 3) and 0.805 mm (LPLI-MACP 1),
677 respectively—are still impressively high, being apparently approached only by
678 *Oppenheimopecten vogdesi* amongst living scallops (Clark 2005). Since these values are from
679 specimens that were evidently rapid growers (half-year increment > 68.7 mm and whole-year
680 increment 116.5 mm, respectively) it might be concluded that rapid growth was brought
681 about by deposition of larger microgrowth increments. However, one must consider the
682 possibility that deposition of increments was more frequent (i.e., on a larger proportion of
683 days). The relationship between half-/whole-year increment size and microgrowth-increment
684 size and number is best examined initially in cases where the half-/whole-year increment size
685 has been precisely defined (from $\delta^{18}\text{O}$ profiles with sufficient summer/winter inflections), but
686 including microgrowth-increment data which does not fully span the relevant half-/whole-
687 year interval. Inclusion of this data boosts sample size and is unlikely to bias mean
688 microgrowth-increment size, although it will of course incorporate underestimates of number.
689 Figure 9A-D shows bivariate plots of this data, revealing fairly good correlations between
690 microgrowth-increment number and half- and whole-year increment size (Fig. 9A, 9C,
691 respectively), but effectively no correlation between mean microgrowth-increment size and
692 half- or whole-year increment size (Fig. 9B, 9D, respectively). Using all the data (i.e.,
693 including minimum estimates for half- and whole-year increment sizes) yields slightly better
694 correlations between microgrowth-increment number and half- and whole-year increment
695 size (Fig. 9E, 9G, respectively), possibly because of the inclusion of shells where the height
696 ranges of microgrowth-increment and $\delta^{18}\text{O}$ profiles are relatively closely matched. However,

697 there is still no correlation between mean microgrowth-increment size and half- or whole-
698 year increment size (Fig. 9F, 9H, respectively). It therefore seems clear that larger half- and
699 whole-year increments (i.e., faster growth rates) generally resulted from deposition of more
700 rather than larger microgrowth increments. Perhaps the fundamental daily rhythm was
701 modulated by the availability of sufficient energetic and material resources to cater for shell
702 secretion as well as soft tissue (including gonad) growth and metabolic needs—i.e., the
703 resources of environments occupied by relatively slow growers only allowed deposition of a
704 new microgrowth increment several days after formation of the previous one. Certainly,
705 deposition is not tied to a one-day periodicity in scallops (Thébault et al. 2006).

706

707 Growth Breaks

708

709 Significant (major and moderate) growth breaks occur over the full height interval of the
710 major microgrowth increment cycle in some of the shells represented in Figures 5–8 (e.g.,
711 LPLI-MACP 2, EPLE-MACP 2). However, in most instances they are concentrated near or at
712 the end, continuing to occur amongst any later (typically small) increments (e.g., LPLI-GCP
713 6). Amongst the shells represented in Figures 5–8, significant growth breaks occur close to
714 the positions of $\delta^{18}\text{O}$ maxima and minima (including the highest maxima and lowest minima)
715 in almost equal proportions, with no difference between GCP and MACP shells. Those
716 occurring at locations away from $\delta^{18}\text{O}$ maxima and minima are not associated with notable
717 changes of profile gradient. They and others may therefore signify only brief interruptions of
718 growth. Amongst the 12 MACP shells studied by Krantz (1990), major growth breaks are
719 associated with the highest $\delta^{18}\text{O}$ maximum in five cases (LPLI-MACP 8, EPLE-MACP 7–10)
720 but with the lowest minimum in only one (EPLE-MACP 4).

721

Winter and Summer Benthic Temperatures

722

723

724 *Preliminary considerations.*—As well as diagenesis, noise and possible misidentification
725 of winter and summer sectors in $\delta^{18}\text{O}$ profiles (see above), ontogenetic and seasonal changes
726 in growth rate (including growth breaks) and profile truncation are matters which must be
727 considered in interpreting seasonal temperatures from $\delta^{18}\text{O}$ data.

728 Ontogenetic decline in growth rate is typical of bivalves and confirmed in *C. eboreus* by
729 the change in form of $\delta^{18}\text{O}$ profiles (generally steeper in late ontogeny). While closer isotopic
730 sampling in late ontogeny no doubt did something to maintain temporal resolution, the higher
731 $\delta^{18}\text{O}$ minima in the second year of growth (five of the six cases where two minima have been
732 recognised; Table 3) suggest that it was not wholly effective: it seems likely that shell
733 material formed at the time of highest temperature was not sampled. We have therefore taken
734 the lowest $\delta^{18}\text{O}$ minimum from each shell (rather than the mean of two values, if available) as
735 representative of summer conditions during the life of the individual and, for consistency of
736 approach, taken the highest $\delta^{18}\text{O}$ maximum as representative of winter conditions, even
737 though no age-related resolution effect is evident amongst winter data.

738 Seasonal change in growth rate (indicated by the relative widths of winter and summer
739 sectors in $\delta^{18}\text{O}$ profiles) and growth breaks are evident in most shells. Growth was usually
740 slower in winter and, like slowing of growth in late ontogeny, may have led to a failure to
741 sample material formed under the most extreme temperatures of the season. Growth breaks
742 associated with $\delta^{18}\text{O}$ maxima and minima may have been of brief duration (see above), such
743 that the measured $\delta^{18}\text{O}$ values are not seriously misrepresentative. However, their higher
744 relative occurrence in association with maxima amongst the MACP shells of Krantz (1990)
745 could have led, in combination with winter slowing of growth, to more frequent
746 underestimation of winter values from these $\delta^{18}\text{O}$ profiles.

747 $\delta^{18}\text{O}$ profiles are truncated at the highest value in EPLI-MACP 2, LPLI-MACP 2, 4 and 5,
748 and EPLE-MACP 1 and 3, and at the lowest value in LPLE-MACP 7 and EPLE-MACP 1, 3
749 and 7. The former and latter sets of cases are likely to provide, respectively, underestimates
750 of extreme winter values and overestimates of extreme summer values. It is noteworthy that
751 all are from the MACP and that probable winter underestimates form the larger proportion.
752 Similar numbers and proportions of cases exist where profiles are truncated near the highest
753 and lowest values (i.e., where the adjacent inflection in the $\delta^{18}\text{O}$ profile may actually
754 represent noise rather than a change in the sign of temperature change). These include a few
755 cases from the GCP, with an equal proportion of possible winter underestimates (LPLI-GCP
756 4, EPLE-GCP 2) and possible summer overestimates (EPLI-GCP 1, LPLI-GCP 2).

757

758 *Seasonal temperatures.*—The following discussion uses temperatures calculated with the
759 preferred water $\delta^{18}\text{O}$ value for the division concerned (Table 3). The full dataset (including
760 temperatures calculated with the other three water $\delta^{18}\text{O}$ values applied in each case) is
761 available online as Supplementary Data File 4.

762 Since they were part of the dataset used at the outset to define the high and low
763 temperature ranges for winter and summer, it is no surprise that 11 of the 12 shells
764 isotopically investigated by Krantz (1990) yield temperatures within the expected categories:
765 HS/HW for LPLI-MACP 8; LS/LW for EPLE-MACP 3–12. That LPLI-MACP 7 does not
766 (falling within the LS/HW category) is a consequence of the use of mean rather than
767 individual data to define the boundary between high and low temperatures, and the fact that
768 the high summer $\delta^{18}\text{O}$ value supplied by this particular specimen is from the end of a profile
769 and almost certainly an overestimate, as already noted by Krantz (1990).

770 Of the other 20 shells considered herein, only eight yield temperatures within the expected
771 category (EPLI-GCP 2; EPLI-MACP 1, 2; LPLI-GCP 2–4; EPLE-MACP 1, 2), the remainder

772 giving temperatures in the low rather than high range for winter and/or summer, with the
773 single exception of EPLE-GCP 1 (yielding a high rather than low summer temperature).
774 Temperatures that are unexpectedly low for winter (EPLI-GCP 1; LPLI-GCP 1, 5, 6; LPLI-
775 MACP 2, 5, 6; EPLE-GCP 2) cannot be the result of slower growth, growth breaks or
776 truncation of $\delta^{18}\text{O}$ profiles, all of which would lead if anything to overestimates of winter
777 temperature. However, these factors might in principle account for lower than expected
778 summer temperatures, so such cases (LPLI-GCP 5, 6; LPLI-MACP 1-7) need to be
779 considered further. In only one (LPLI-MACP 7) is the summer $\delta^{18}\text{O}$ value involved from an
780 atypical (narrow) summer sector or the end/near-end of a profile, and in three of the others
781 (LPLI-GCP 5; LPLI-MACP 4, 6) there is no significant growth break associated. Growth
782 breaks are, however, located close to the positions of the lowest $\delta^{18}\text{O}$ values in LPLI-GCP 6,
783 LPLI-MACP 1-3 and LPLI-MACP 5. It is doubtful whether temperatures well below the HS
784 range (LPLI-GCP 6; LPLI-MACP 1; LPLI-MACP 2; LPLI-MACP 7:) reflect overestimation
785 of $\delta^{18}\text{O}$ as a consequence of truncation or growth breaks. However, where summer
786 temperatures are just below the HS/LW boundary (LPLI-MACP 3; LPLI-MACP 5) this is a
787 distinct possibility. LPLI-MACP 3 may, therefore, have lived under HS/HW conditions and
788 LPLI-MACP 5 under HS/LW conditions. LPLI-GCP 4, LPLI-MACP 1, 3 and 4, and EPLE-
789 GCP 1 yield winter temperatures within the HW range, as expected, but the values concerned
790 are within 1 °C of the HW/LW threshold and correspond to $\delta^{18}\text{O}$ values from positions near
791 to growth breaks and/or the ends of profiles. It is therefore possible that temperatures fell to
792 values within the LW range. The general picture is of temperatures according with
793 expectation or lower, there being just one example of a higher (summer) temperature than
794 expected, two examples where a more complete $\delta^{18}\text{O}$ record might have yielded a higher
795 (summer) temperature than expected, and a further five examples where a more complete
796 $\delta^{18}\text{O}$ record might have yielded a lower (winter) temperature than expected.

797 While the seasonal temperatures calculated from shells are changed if the value for water
798 $\delta^{18}\text{O}$ is altered, the discrepancies with expectation identified above remain if the expected
799 temperatures are recalculated with the altered value for water $\delta^{18}\text{O}$ (not applicable to EPLI-
800 GCP, where the expected temperatures are based on assemblage composition). It is
801 nevertheless worth examining the influence of water $\delta^{18}\text{O}$ on the absolute temperatures
802 obtained from shells. Winter and summer temperatures calculated using an arbitrary common
803 value of water $\delta^{18}\text{O}$ (+0.7‰) are presented in Table 3 for comparison with those calculated
804 using the preferred values. The effect of a common water $\delta^{18}\text{O}$ on divisional mean
805 temperatures is to make the EPLE-GCP winter temperature relatively high and the other
806 winter temperatures relatively low, and the LPLI-GCP, EPLE-GCP and EPLE-MACP
807 summer temperatures relatively high and the EPLI-GCP, EPLI-MACP and LPLI-MACP
808 summer temperatures relatively low. While ostracod and mollusk assemblages provide
809 independent evidence of warm conditions for the EPLE-MACP division, the indicated
810 temperatures are little or no higher than in the LPLI-MACP division (Hazel 1971, 1988;
811 Ward et al. 1991). More significantly, ostracod and mollusk assemblages, together with
812 foram assemblages (Dowsett and Wiggs 1992), provide compelling evidence that
813 temperatures were substantially higher in the LPLI-MACP division than in the EPLI-MACP
814 division, in notable contrast to $\delta^{18}\text{O}$ data from *C. eboreus* employed with a common value of
815 water $\delta^{18}\text{O}$. It is evident from this analysis that water $\delta^{18}\text{O}$ has a considerable impact on
816 estimated temperature, but also clear that use of a common value is inappropriate. We made
817 informed choices for each division (see above) but recognise that it would be worth applying
818 additional methods to constrain water $\delta^{18}\text{O}$. ‘Clumped isotope’ (Δ_{47}) analysis (e.g.,
819 Winkelstern et al. 2017) and the $\delta^{18}\text{O}$ of homeotherm phosphate (e.g., Walliser et al. 2015;
820 Ciner et al. 2016) are promising tools.
821

Growth Rate-Environment Relationships

822

823

824 Based on their largest half-year (hy) and whole-year (wy) increment sizes we have
825 assigned shells to growth-rate classes as follows: Slow (hy < 30 mm, wy < 60 mm); Medium
826 (hy > 30 mm, wy > 60 mm); Fast (hy > 60 mm, wy > 90 mm); Very Fast (hy > 90 mm, wy >
827 120 mm). In cases of conflict between half- and whole-year data we have assigned shells to
828 the faster growth-rate class indicated. The growth-rate distribution amongst the 32 shells is 9
829 Slow, 14 Medium, 5 Fast, 4 Very Fast. Shells in the Slow class are restricted to the MACP
830 and those in the Very Fast class to the GCP. Figure 10 locates the shells, segregated by
831 growth rate, within the temperature/primary production matrix previously generated (Fig. 4),
832 but in positions informed by the isotopic data obtained from them. As indicated above, $\delta^{18}\text{O}$
833 data places many shells in a different temperature category to that expected, and more
834 complete records might have had the same effect for a number of other shells. The latter
835 possibility is indicated by a second entry in smaller typeface at the appropriate position. The
836 same approach is used with respect to production category in the cases of EPLE-GCP 1 and
837 2, for which $\delta^{13}\text{C}$ data provides some evidence of high rather than 'average' production.
838 Otherwise, we have assigned shells to the production category indicated by the associated
839 fauna (see above).

840 Reasoning from the growth-rate predictions set out earlier, and defining 'rapid' growth as
841 a rate within the Very Fast class (faster growth than in any other scallop species), the
842 existence of examples (LPLI-GCP 5, 6) from the LS/LW temperature category rules out
843 temperature control of growth. The existence of an example (EPLE-GCP 1) from the
844 'average' production category appears to rule out production control as well. However, the
845 growth rate of this specimen is only just in the Very Fast class and, as we have noted, $\delta^{13}\text{C}$
846 evidence from the division concerned (and this specimen in particular) provides some

847 grounds for thinking that production may have been high rather than 'average'. Defining
848 'rapid' more broadly to include the Fast growth-rate class gives a more ambiguous picture:
849 two definite examples and one possible are added from the LS/LW temperature category but
850 also three definite examples from the 'average' production category. This is, however,
851 consistent with the environmental associations of modern scallops in the Fast growth-rate
852 class: populations of *Y. balloti* and *A. purpuratus* exhibiting this rate of growth occur in areas
853 of 'average' phytoplankton production (FAO 1981, map 1.1) in north-eastern Australia and
854 northern Chile, respectively (Williams and Dredge 1981; DiSalvo et al. 1984).

855 That there are a number of examples of Medium growth rate from the high production
856 category does not refute the notion of production-controlled growth: some variation in growth
857 rate is to be expected due to short-term fluctuations in production and to individual
858 differences in the ability to respond to high food supply. Moreover, the proportion of
859 examples of Medium growth rate relative to cases of Fast and Very Fast growth rate is no
860 lower in the HS/HW than in the LS/LW temperature category, contrary to what one would
861 expect for temperature-controlled growth. Support for production-controlled growth comes
862 from the complete absence of examples of Slow growth from the high production category, in
863 contrast to many from the 'average' production category. Amongst the latter, however, all but
864 one are from the LS/LW temperature category. The $\delta^{18}\text{O}$ profile of the sole exception (LPLI-
865 MACP 7) is short, apparently including a winter maximum (giving a temperature in the high
866 winter range) but not showing a summer inflection and therefore providing only a minimum
867 estimate (> 20 mm) for half-year increment. The growth rate of this specimen might therefore
868 actually have been in the Medium class. Not only are there many in the Slow growth-rate
869 class within the LS/LW temperature category, the winter minimum temperatures supplied are
870 notably low: four of eight below 7°C (Table 3) compared with none as low as this amongst
871 the six Medium–Very Fast growers from the same temperature category under high or

872 possibly high production. The winter temperature supplied by the Very Fast grower LPLI-
873 GCP 1, also from a high production setting but in the HS/LW temperature category, is also
874 relatively high (11.3 °C). In this case there is no growth break associated with the winter
875 temperature minimum, but one is present in the other specimens from high production/low
876 winter temperature settings. These individuals may therefore have experienced (but not
877 recorded) winter temperatures approaching those indicated by some of the Slow growers in
878 the LS/LW temperature category and ‘average’ production category. By their very existence,
879 however, winter growth breaks (and the slowing of growth in this season) show some control
880 of growth by temperature as well as production. Such breaks are more common than summer
881 growth breaks amongst shells from the EPLE-MACP division, from which all definite
882 examples of Slow growth derive. It is therefore reasonable to conclude that these examples
883 reflect the influence of low winter temperature, in addition to ‘average’ production.

884

885 CONCLUSIONS AND FURTHER WORK

886

887 We have shown that *C. eboreus* lived no longer than two years but in some cases grew
888 exceedingly rapidly (by depositing more rather than larger microgrowth increments) to reach
889 an unusually large size. Growth typically slowed in winter, when mortality was relatively
890 high, and in late ontogeny. Individuals surviving long enough to spawn may then have
891 suffered a ‘programmed’ death. Post-larval growth started in the spring or summer in the
892 MACP, but sometimes in the fall or winter in the GCP; growth interruptions occurred in
893 summer and winter in both areas, but more commonly in winter in the former. As well as
894 these geographic differences in life history, overall growth rate varied with specific aspects of
895 the environment (primary production and temperature).

896 On the basis of growth rate-environment relationships we may interpret the extinction of
897 *C. eboreus* as a result of the combined impact of declines in primary production and
898 temperature, specifically winter temperature. The lower growth rate associated with these
899 changes would have increased mortality through predation by preventing rapid achievement
900 of the refuge offered by large size. This might have led to a progressive reduction in overall
901 population size. The lack of impact of low temperature on growth under conditions of high
902 production implies that extinction would not have occurred had these conditions been
903 maintained. On the other hand, the evident impact of low temperature on growth under
904 ‘average’ production suggests that if temperature had been maintained, reduced production
905 might have been insufficient to cause extinction. The survival (in abundance) of *C. eboreus* in
906 the MACP long after the fall in production within the Pliocene seems to confirm that
907 temperature decline was contributory to extinction. However, it is puzzling that the species
908 continued deep into the Pleistocene, by which time there had been numerous, increasingly
909 severe, episodes of refrigeration in the North Atlantic region (McClymont et al. 2013). There
910 is some evidence for a Pleistocene reduction in predation intensity on bivalves in the GCP
911 (Mondal et al. 2014) but not in the MACP (Sime and Kelley 2016), so it cannot be argued
912 that growth-related decline in the ability of *C. eboreus* to survive predatory attacks was offset
913 by less frequent encounters with predators. Perhaps the continuation of the species reflects
914 localised persistence of high production and/or the time required for disruption of once-
915 ubiquitous high production over the geographic range of *C. eboreus* to bring about the demise
916 of all populations. Certainly, the effects of habitat fragmentation and reduction are not
917 immediate, and (counter-intuitively) extinction of competitively inferior species may be
918 especially delayed (Nee and May 1992; Tilman et al. 1994). Short larval life also confers
919 resistance to extinction in scallops (Smith and Jackson 2009). The competitive status of *C.*
920 *eboreus* would be difficult to determine but duration of the larval stage is straightforward

921 (Smith et al. 2003). As well as the latter, it would be well worth investigating the growth rate
922 and environment of the very latest recorded specimens, from the Flanner Beach and
923 Canepatch formations. Individuals up to 156 mm in height are known (Ward 2008, pl. 16,
924 figs. 1, 2), a size reached earlier only under high production, hence these examples might
925 evince the localised persistence of such conditions, as hypothesised above. Demonstration of
926 rapid growth by the techniques employed herein would support this interpretation, and it
927 might be confirmed (in the absence of assemblage evidence) by various other geochemical
928 approaches (e.g., Krantz et al. 1988; Haveles and Ivany 2010; Thébault and Chauvaud 2013;
929 Georgiev et al. 2015). Conceivably, the indications from the latter might be that production
930 was high, from $\delta^{18}\text{O}$ and microgrowth-increment profiles that growth was slow, and from
931 absolute $\delta^{18}\text{O}$ values that temperature was low. This would lend support to the involvement
932 of temperature decline in extinction whilst also maintaining a role for production decline.
933 Temperature estimates from shell $\delta^{18}\text{O}$ would, however, be subject to the same uncertainty as
934 those obtained from older material herein. For this reason, incorporation of the additional (but
935 still isotope-based) approaches advanced earlier would be beneficial. Indeed, the conclusions
936 reached from the present study are to some extent dependent on the accuracy of the
937 temperatures determined, and these therefore urgently need validation by the additional
938 approaches advocated. If it were shown that EPLE-MACP specimens in the Slow growth-rate
939 class lived under warm winter conditions (in agreement with mollusk- and ostracod-
940 assemblage evidence but contrary to the $\delta^{18}\text{O}$ -derived temperatures supplied herein), it would
941 remove the case for some involvement of temperature decline in the extinction of *C. eboreus*.

942 Ultimately, companion sclerochronological studies of other taxa will be required to
943 formulate a general theory of Plio-Pleistocene bivalve extinction on the US eastern seaboard.
944 As indicated at the outset, hundreds of species became extinct, and *C. eboreus* may constitute
945 an exception in having been adversely affected by reduced primary production. However, the

946 same cause has been invoked for the selective demise of a large, fast-growing *Crassostrea*
947 species in the Pliocene of the Caribbean (Kirby and Jackson 2004) and might also apply to
948 the extinction of *Chesapecten*, a further large, fast-growing scallop taxon (Goewert and Surge
949 2008), in the Pliocene of the US eastern seaboard. Other large taxa survived from the
950 Pliocene to present. Possibly these were unaffected by reduced production as a result of a
951 life-history strategy involving slow growth and long life. Such a strategy might have been
952 advantageous (enabling greater investment in reproduction) if the predators of these taxa
953 were not deterred by large size. In *Mercenaria*, several species of which survived from the
954 Pliocene to present, large size does offer a refuge from predation (Dietl 2003), so slow
955 growth would have been disadvantageous. Whether large size has benefits in other taxa is in
956 most cases only surmised. Certainly, sclerochronological studies will need to be accompanied
957 by aut- and synecological investigations (cf. Dietl et al. 2004; O’Dea and Jackson 2009;
958 Smith and Jackson 2009; Leonard-Pingel et al. 2012; Leonard-Pingel and Jackson 2016;
959 Sime and Kelley 2016) for a full understanding of Plio-Pleistocene bivalve extinction on the
960 US eastern seaboard.

961

962

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1375

1376

FIGURE CAPTIONS

1377

- 1378 FIG. 1.—Specimens of *Carolinapecten eboreus* and an example of the extant scallop
 1379 *Aequipecten opercularis* from the Pliocene of the UK, showing overall morphology,
 1380 microgrowth increments, and the positions of growth breaks and certain $\delta^{18}\text{O}$ values. **A)** *C.*
 1381 *eboreus* LPLI-GCP 5 (right valve; Very Fast growth rate). **B)** *C. eboreus* LPLI-GCP 3 (left
 1382 valve; Fast growth rate). **C)** *C. eboreus* EPLE-MACP 1 (right valve; Medium growth rate).
 1383 **D)** *A. opercularis* UD 52795 (right valve). **E)** Enlargement of area indicated in B. **F)**

1384 Enlargement of area indicated in C. **G)** Enlargement of area indicated in D. Scale bars
1385 (vertical: A–D; horizontal: E–G) = 10 mm. S1/2 and W1/2 in A–D mark the positions of
1386 extreme summer and winter $\delta^{18}\text{O}$ values, respectively ($\delta^{18}\text{O}$ data for D in Johnson et al. 2009,
1387 fig. 8A). Other symbols in A–C signify the points between which the largest whole-year
1388 increments (green circles) and largest half-year increments (purple semicircles; superimposed
1389 on green circle where whole- and half-year increment boundaries coincide) were measured on
1390 the basis of $\delta^{18}\text{O}$ profiles (Figs. 6E, 6C and 8D, respectively), and the positions of major
1391 (filled blue triangles) and moderate (open blue triangle) growth breaks (see also F for the
1392 form of major growth breaks). Since the shell in C is incomplete, measurements were
1393 mathematically adjusted (see text) to correspond to measurements along the mid-line
1394 (anatomical height). The size of the microgrowth increments (bounded by commarginal
1395 lamellae) in F is similar to those in G (*A. opercularis*), and in other scallop species (e.g.,
1396 Owen et al. 2002). Note the very much larger microgrowth increments in E. Although these
1397 are at the high end of the size-range in *C. eboreus*, microgrowth increments only slightly
1398 smaller are typical of the species (Table 2).

1399

1400 FIG. 2.—Chronostratigraphic position (age in Ma) of EPLI (brown), LPLI (pink) and EPLE
1401 (light blue) *C. eboreus* specimens, with corresponding museum accession numbers and/or
1402 specimen codes of Krantz (1990) and Jones and Allmon (1995). Broad age estimates for the
1403 source units are signified by thin lines; more precise (but not necessarily accurate) estimates
1404 by thick lines (double thickness where two estimates coincide). In some cases there were
1405 imprecise and/or alternative source units, signified by dashed lines. Source units indicated in
1406 the text; details, together with evidence of age, in Supplementary Data File 1.

1407

1408 FIG. 3.—Geographic provenance of *C. eboreus* specimens (see text for names of locations).

1409

1410 FIG. 4.—Temperature and production characteristics of time-space divisions recognised
1411 herein, based on earlier studies (see text).

1412

1413 FIG. 5.—Data for $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, microgrowth-increment height and growth-break position from
1414 EPLI-GCP and EPLI-MACP specimens of *C. eboreus*. **A)** EPLI-GCP 1. **B)** EPLI-MACP 1.
1415 **C)** EPLI-GCP 2. **D)** EPLI-MACP 2. Isotope data represented by crosses = replicate analyses
1416 for a given position, the mean or most reasonable single value being used in the relevant
1417 profile (line). Dashed line for microgrowth-increment height = raw data; continuous line = 5-
1418 point averages. Filled and open triangles (blue) = major and moderate growth breaks,
1419 respectively. Semicircles (purple) and circles (green) = $\delta^{18}\text{O}$ values defining the largest half-
1420 and whole-year increments, respectively (semicircles superimposed on circles where
1421 boundaries of half- and whole-year increments coincide). S1/2 and W1/2 = summers and
1422 winters, respectively, as identified from the $\delta^{18}\text{O}$ profiles. Isotopic axis reversed so that lower
1423 values of $\delta^{18}\text{O}$ (representative of higher temperatures) plot towards the top.

1424

1425 FIG. 6.—Data for $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, microgrowth-increment height and growth-break position from
1426 LPLI-GCP specimens of *C. eboreus*. **A)** LPLI-GCP 1. **B)** LPLI-GCP 2. **C)** LPLI-GCP 3. **D)**
1427 LPLI-GCP 4. **E)** LPLI-GCP 5. **F)** LPLI-GCP 6. Symbols and format explained in Figure 5,
1428 with the exception of stars (marking aberrant early ontogenetic $\delta^{18}\text{O}$ values, thought to reflect
1429 diagenetic alteration; see text).

1430

1431 FIG. 7.—Data for $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, microgrowth-increment height and growth-break position from
1432 LPLI-MACP specimens of *C. eboreus*. **A)** LPLI-MACP 1. **B)** LPLI-MACP 2. **C)** LPLI-

1433 MACP 3. **D)** LPLI-MACP 4. **E)** LPLI-MACP. **F)** LPLI-MACP 6. Symbols and format
1434 explained in Figures 5 and 6.

1435

1436 FIG. 8.—Data for $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, microgrowth-increment height and growth-break position from
1437 EPLE-GCP and EPLE-MACP specimens of *C. eboreus*. **A)** EPLE-GCP 1. **B)** EPLE-MACP
1438 1. **C)** EPLE-GCP 2. **D)** EPLE-MACP 2. Symbols and format explained in Figure 5.

1439

1440 FIG. 9.—Number and mean size (height) of microgrowth increments versus size (height) of
1441 the largest half- and whole-year increment in *C. eboreus* specimens (data from Table 2). **A)**
1442 Number of microgrowth increments per half-year increment in specimens whose $\delta^{18}\text{O}$
1443 profiles have summer/winter inflections precisely defining the largest half-year increment. **B)**
1444 as A but for mean size of microgrowth increments. **C)** As A but for whole-year increments.
1445 **D)** As B but for whole-year increments. **E)** As A but with the addition of specimens whose
1446 $\delta^{18}\text{O}$ profiles have insufficient inflections to precisely define the largest half-year increment,
1447 providing only minimum estimates. **F)** As E but for mean size of microgrowth increments. **G)**
1448 As E but for whole-year increments. **H)** As F but for whole-year increments.

1449

1450 FIG. 10.—Growth rate of shells in relation to $\delta^{18}\text{O}$ -derived summer and winter temperatures
1451 (referred to the categories identified in Fig. 4) and primary production (inferred from the
1452 associated biota). Second entries in smaller typeface represent alternative interpretations of
1453 seasonal temperature (where the $\delta^{18}\text{O}$ profile was of insufficient length to provide conclusive
1454 evidence) and/or production (from $\delta^{13}\text{C}$ evidence); see text for further information. The ‘flat’
1455 $\delta^{18}\text{O}$ profile from LPLI-GCP 3 (Fig. 6C) is interpreted as a high temperature winter record
1456 (see text); in the absence of a summer record, classification in terms of seasonal temperature

1457 can only be partial, as indicated by the two entries in parentheses and the same (standard)
1458 typeface, signifying equal probability.

1459

1460

TABLE CAPTIONS

1461

1462 TABLE 1.—Winter minimum and summer maximum temperatures calculated from the shell
1463 $\delta^{18}\text{O}$ of various bivalve mollusk genera from ‘early Pliocene’ (EPLI), ‘late Pliocene’ (LPLI)
1464 and early Pleistocene (EPLI) stratigraphic units of the Middle Atlantic Coastal Plain (see
1465 Supplementary Data File 1 for evidence of age). Superscripts indicate the source of the $\delta^{18}\text{O}$
1466 data: a = Krantz (1990); b = Goewert and Surge (2008); c = Winkelstern et al. (2013); d =
1467 Johnson et al. (2017). The figures given are based on the largest maximum (winter) and
1468 smallest minimum (summer) $\delta^{18}\text{O}$ values from individual profiles; the corresponding
1469 individual seasonal temperatures were either those supplied by the original authors
1470 (Winkelstern et al. 2013; Johnson et al. 2017) or values recalculated as specified in Johnson
1471 et al. (2017) or herein (see text). Water $\delta^{18}\text{O}$ values of +0.70‰ (EPLI), +1.10‰ (LPLI) and
1472 0.00‰ (EPLI) were used.

1473

1474 TABLE 2.—Size (height) of the largest half- and whole-year increments in specimens of *C.*
1475 *eboreus* (as measured from $\delta^{18}\text{O}$ profiles), together with the number and mean size (height) of
1476 microgrowth increments in these half- and whole-year increments (where determined). Key
1477 to superscripts (sources of shell $\delta^{18}\text{O}$ data): a = this study; b = Jones and Allmon (1995, fig.
1478 10); c = Krantz (1990, figs. 4b, 5b, 6–8).

1479

1480 TABLE 3.—Individual and divisional mean winter and summer temperatures calculated using
1481 the largest maximum (winter) and smallest minimum (summer) values of shell $\delta^{18}\text{O}$ from

1482 each specimen (see Supplementary Data File 4), in combination with the preferred value of
1483 water $\delta^{18}\text{O}$ for the division concerned (see text) and an arbitrary common value (+0.7‰).

1484 Key to superscripts (sources of shell $\delta^{18}\text{O}$ data): a = this study; b = Jones and Allmon (1995,
1485 fig. 10); c = Krantz (1990, tables 3–5).

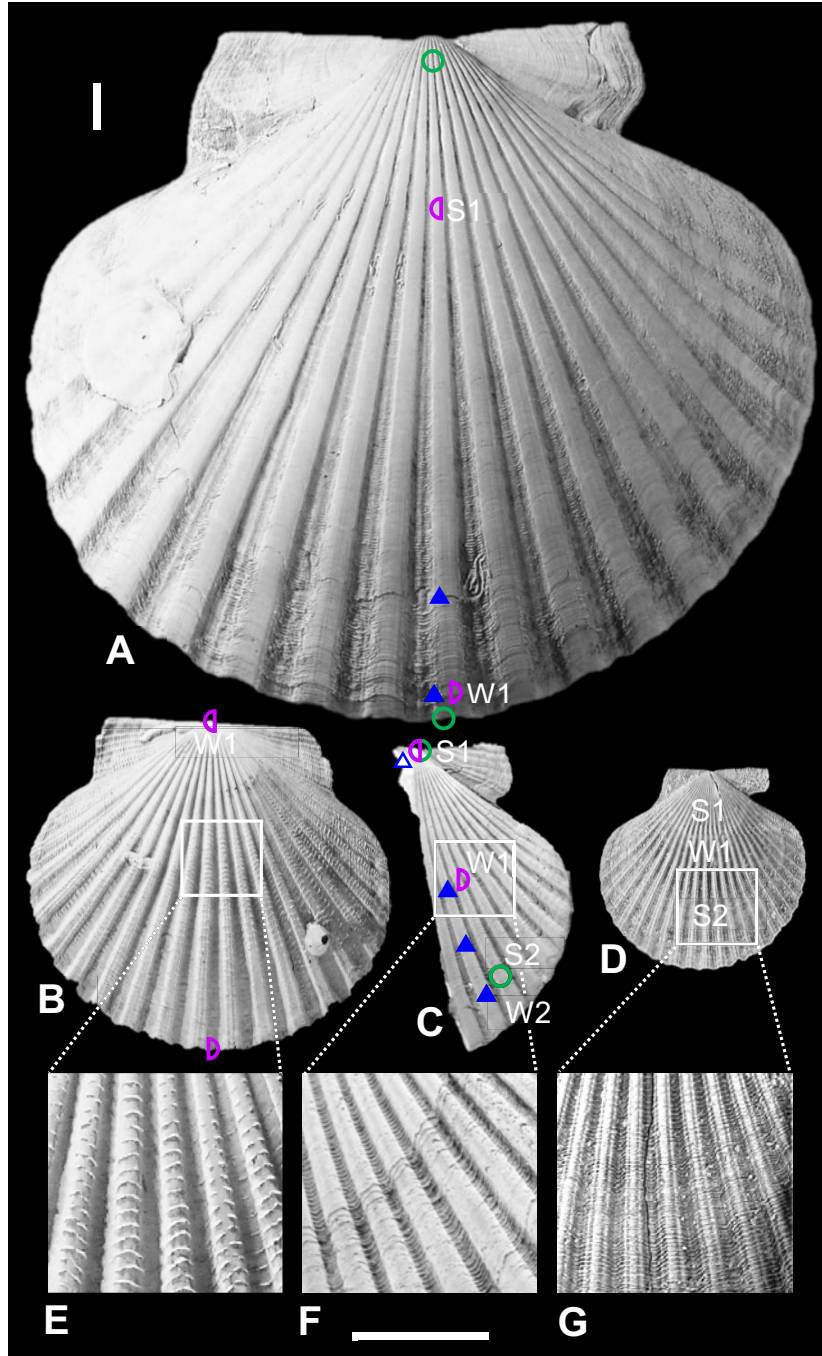
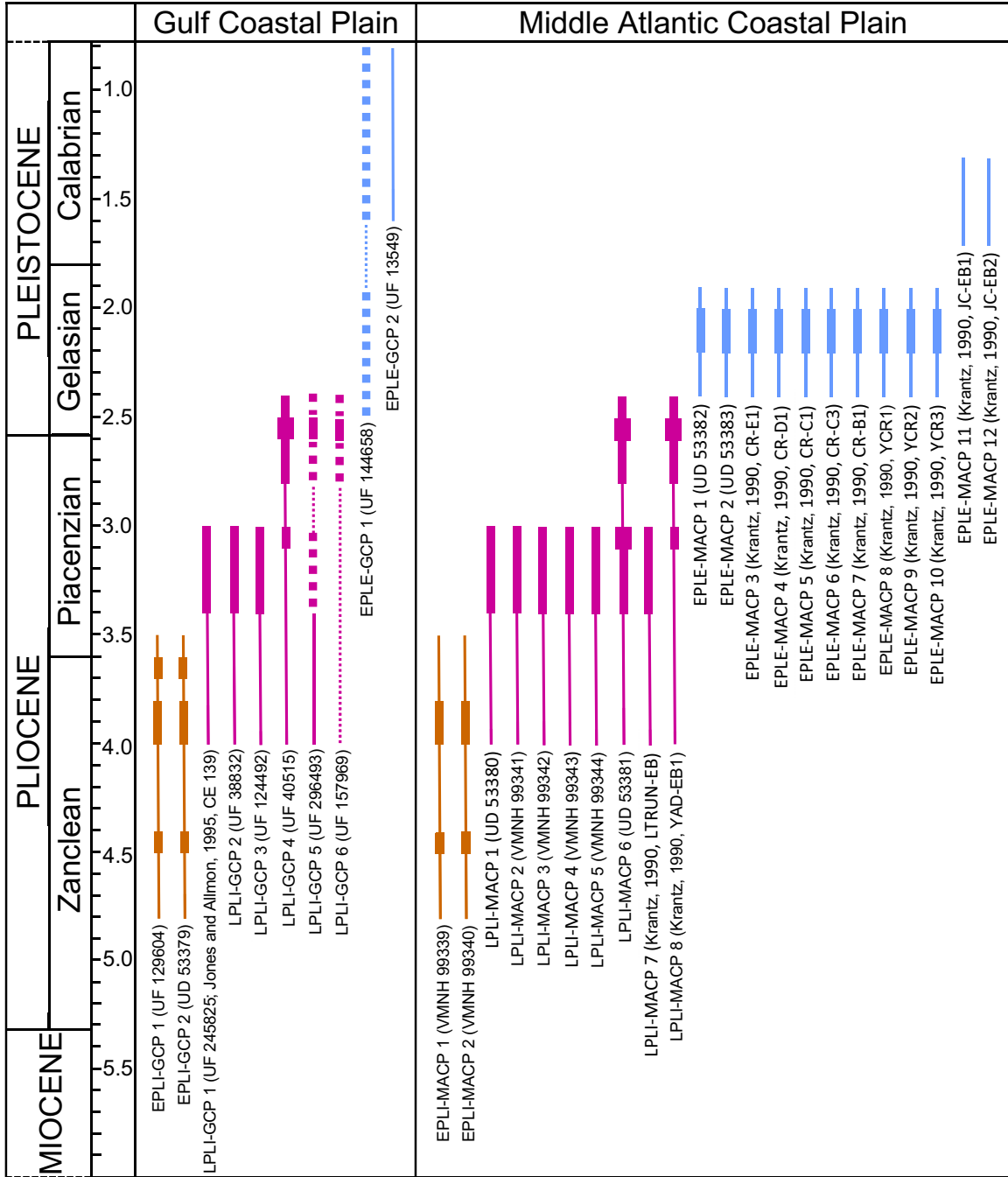


FIGURE 1

FIGURE 2



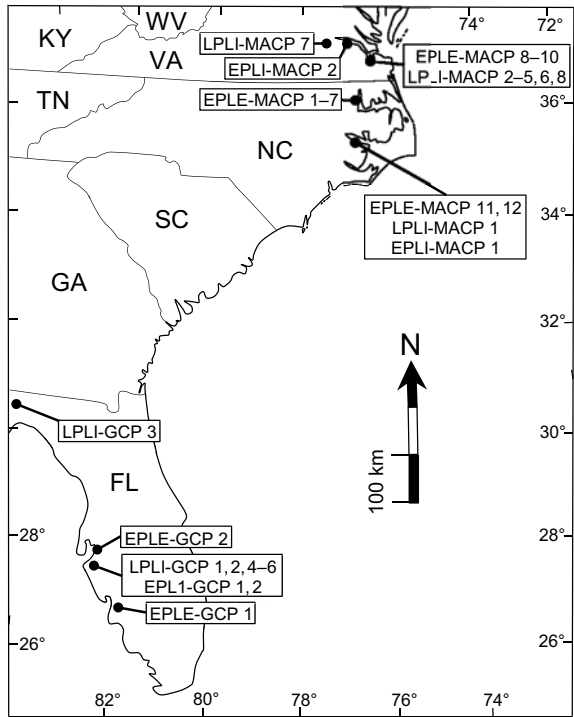


FIGURE 4

Temperature	Primary production	
	'Average'	High
High summer (HS): ≥ 24 °C High winter (HW): ≥ 11.5 °C	LPLI-MACP	LPLI-GCP
High summer (HS): ≥ 24 °C Low winter (LW): < 11.5 °C		
Low summer (LS): < 24 °C High winter (HW): ≥ 11.5 °C	EPLI-GCP	EPLI-GCP
Low summer (LS): < 24 °C Low winter (LW): < 11.5 °C	EPLI-MACP	EPLI-MACP

FIGURE 5

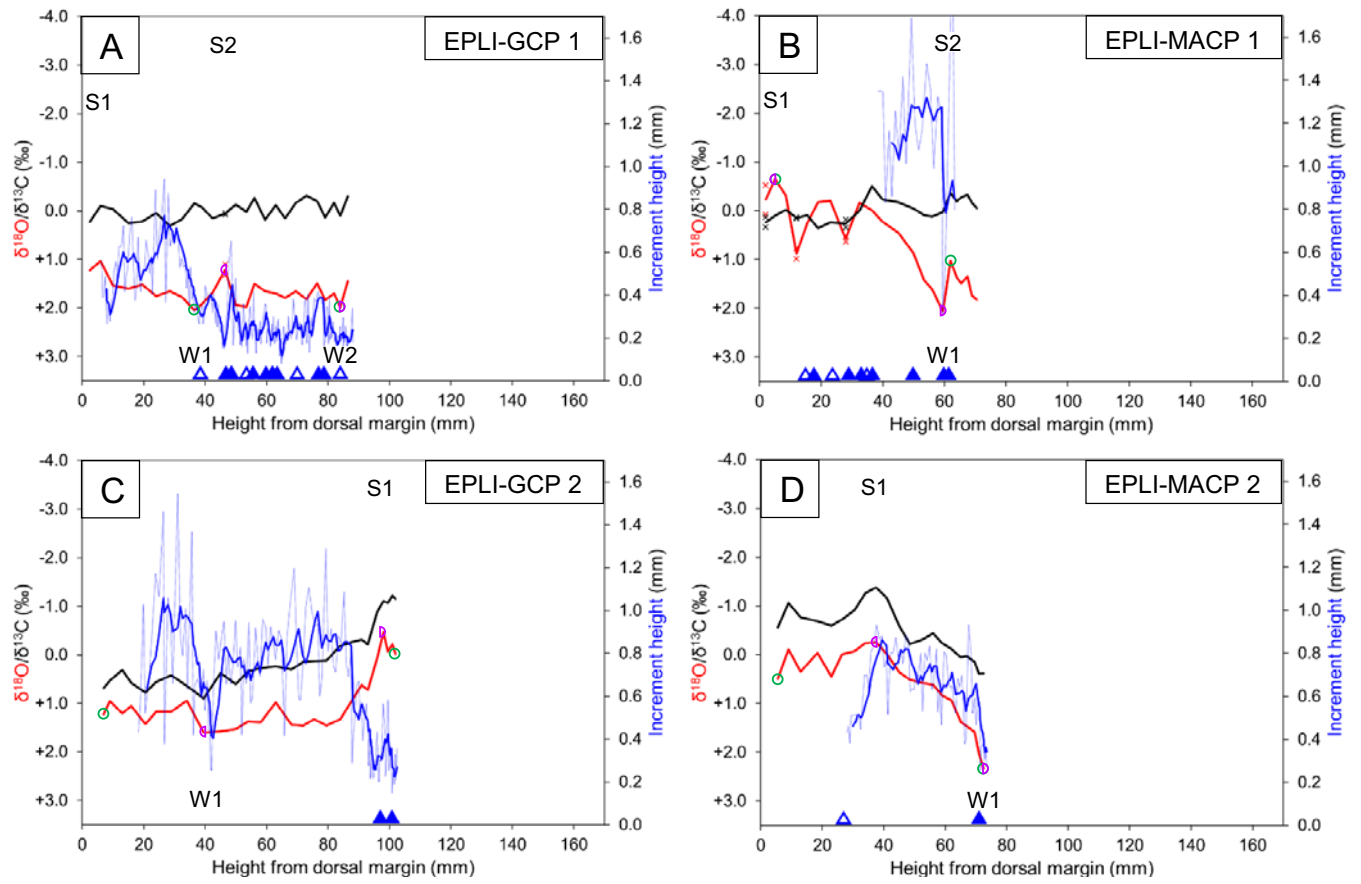


FIGURE 6

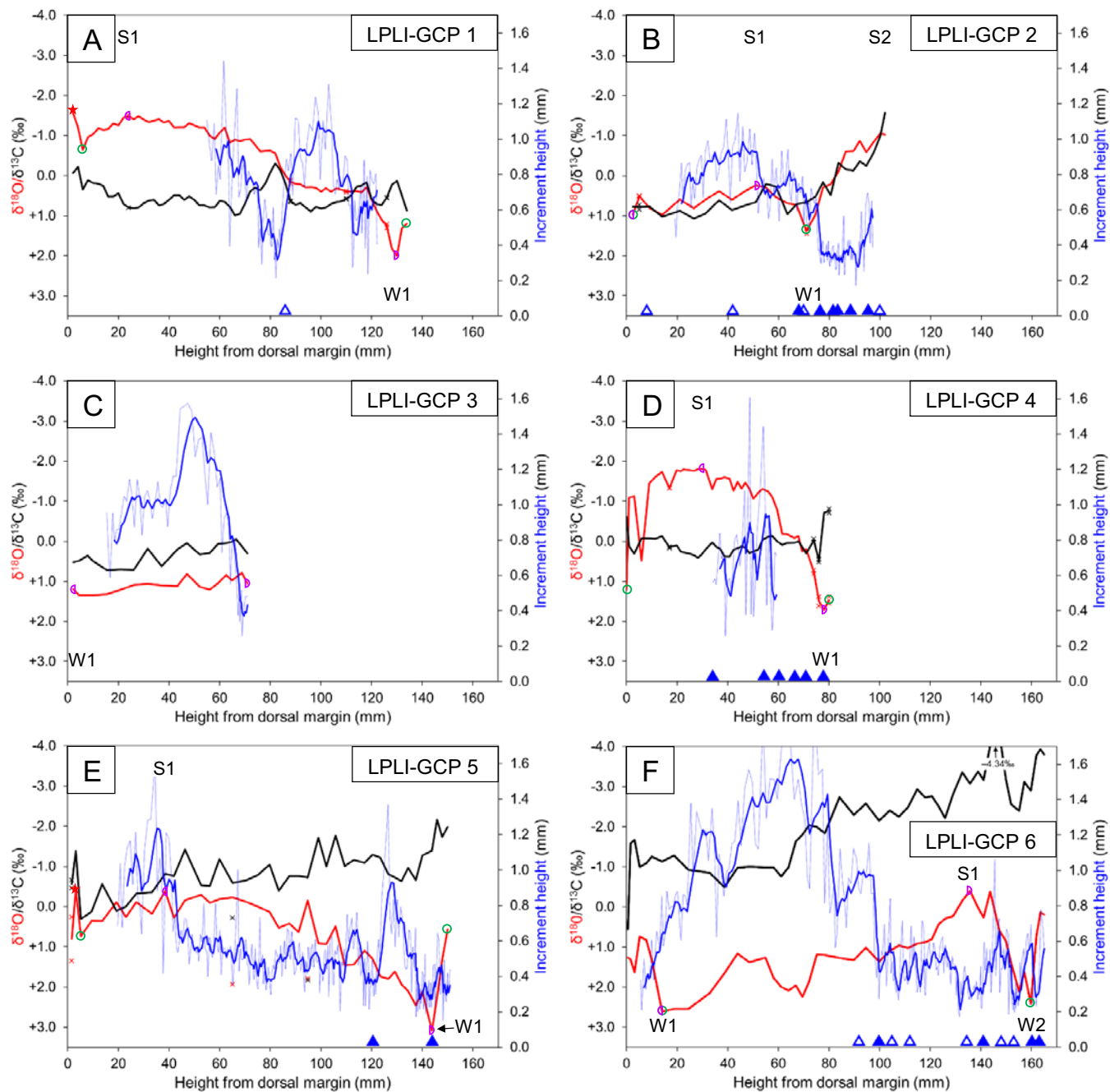


FIGURE 7

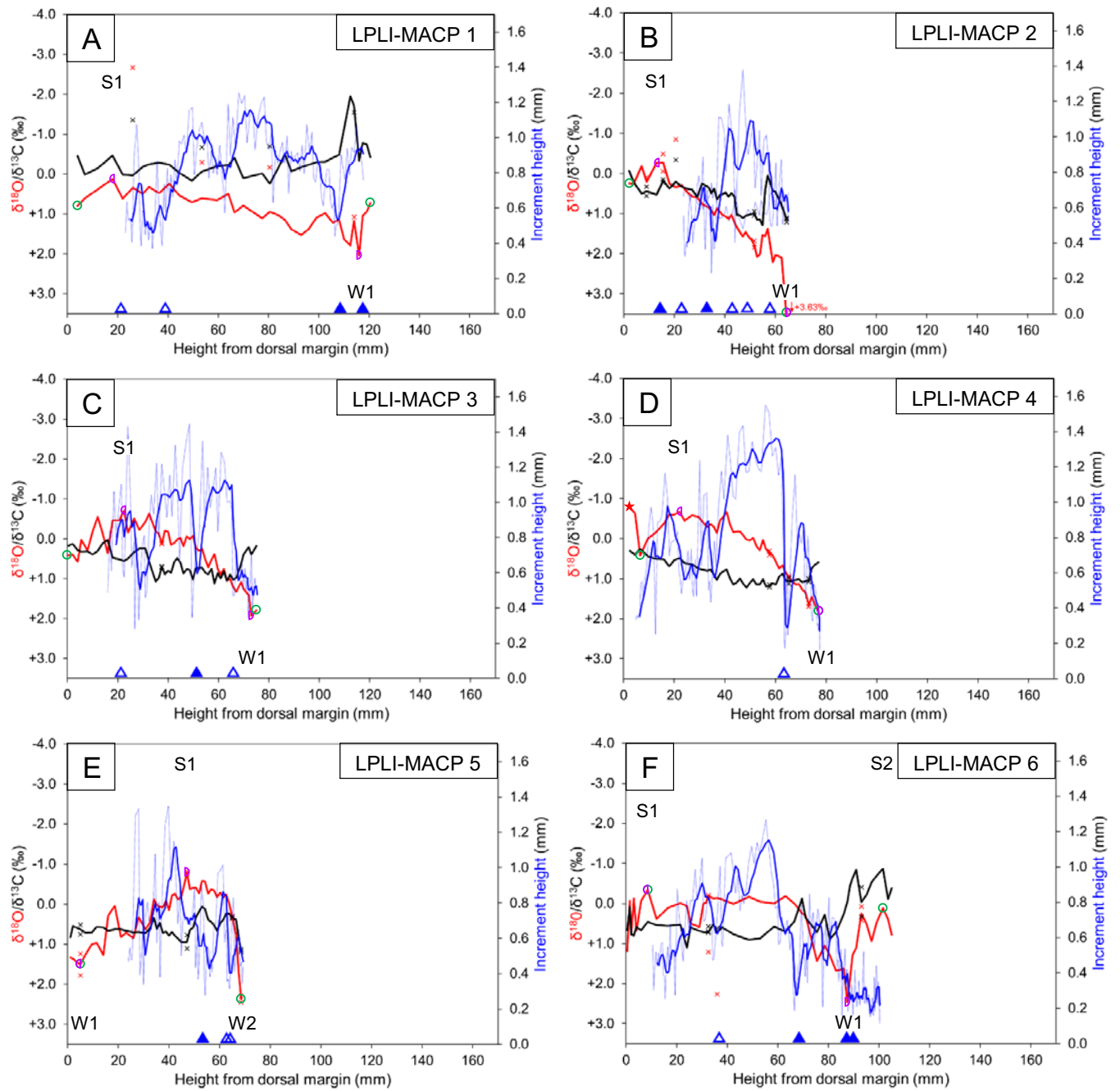
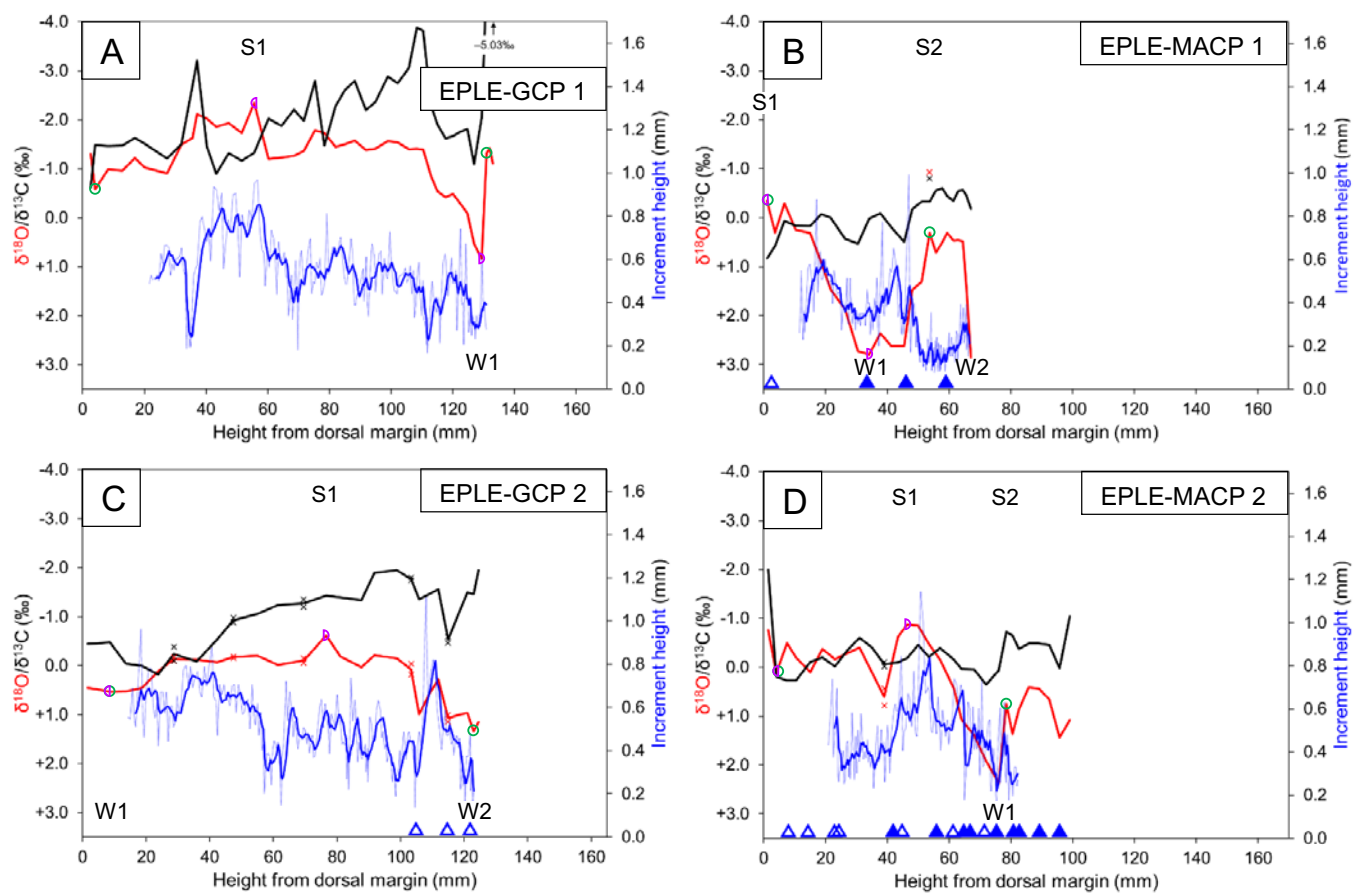


FIGURE 8



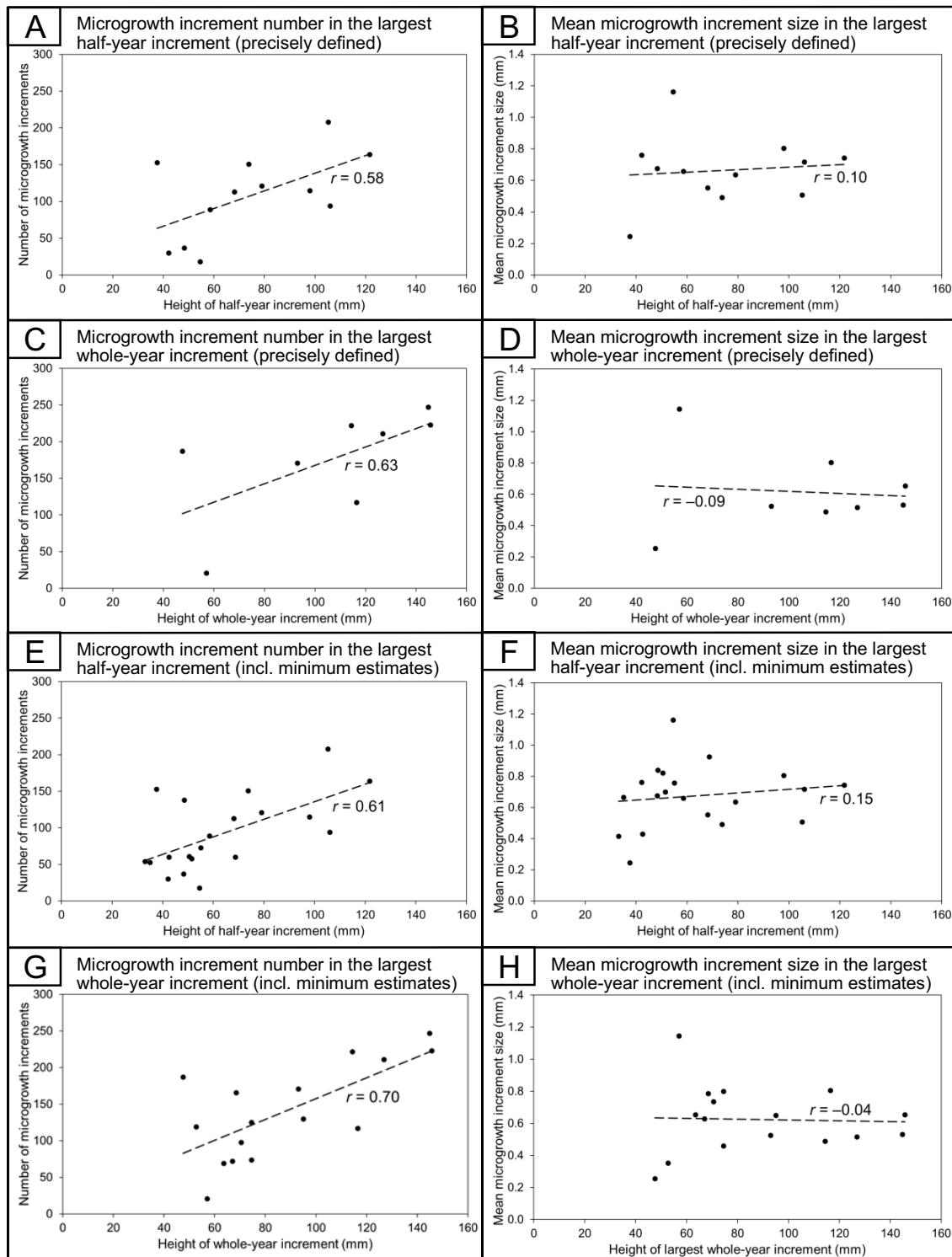


FIGURE 9

Temperature	'Average' primary production				High primary production			
	Growth rate				Growth rate			
	Slow ½-yr: < 30 mm 1-yr: < 60 mm	Medium ½-yr: > 30 mm 1-yr: > 60 mm	Fast ½-yr: > 60 mm 1-yr: > 90 mm	Very Fast ½-yr: > 90 mm 1-yr: > 120 mm	Slow ½-yr: < 30 mm 1-yr: < 60 mm	Medium ½-yr: > 30 mm 1-yr: > 60 mm	Fast ½-yr: > 60 mm 1-yr: > 90 mm	Very Fast ½-yr: > 90 mm 1-yr: > 120 mm
HS/HW	LPLI-MACP 7	LPLI-MACP 3 LPLI-MACP 8		EPLI-GCP 1		LPLI-GCP 2 LPLI-GCP 4	(LPLI-GCP 3)	EPLI-GCP 1
HS/LW		LPLI-MACP 5		EPLI-GCP 1		LPLI-GCP 4		LPLI-GCP 1
LS/HW	LPLI-MACP 7	LPLI-MACP 3 LPLI-MACP 4	LPLI-MACP 1				EPLI-GCP 2 (LPLI-GCP 3)	
LS/LW	EPLI-MACP 4 EPLI-MACP 5 EPLI-MACP 6 EPLI-MACP 8 EPLI-MACP 9 EPLI-MACP 10 EPLI-MACP 11 EPLI-MACP 12	LPLI-MACP 2 LPLI-MACP 3 LPLI-MACP-4 LPLI-MACP 5 EPLI-MACP 1 EPLI-MACP 2 EPLI-MACP 3 EPLI-MACP 7				EPLI-GCP 1 EPLI-MACP 1 EPLI-MACP 2	EPLI-GCP 2	LPLI-GCP 5 LPLI-GCP 6

FIGURE 10

TABLE 1

Age	Formation	Member	Genus	Winter minimum temperature (°C)		Summer maximum temperature (°C)	
				Mean value ± 1σ (n)	Singleton value	Mean value ± 1σ (n)	Singleton value
EPLI	James City Fm (lower)		<i>Carolinapecten</i> ^a	6.6 ± 0.9 (2)		19.8 ± 0.5 (2)	
	Chowan River Formation		<i>Carolinapecten</i> ^a	7.5 ± 1.6 (8)		20.8 ± 1.9 (8)	
			<i>Mercenaria</i> ^c	10.5 ± 0.5 (6)		22.0 ± 2.2 (6)	
LPLI	Yorktown Formation (upper)	Moore House	<i>Carolinapecten</i> ^a		14.5		26.8
			<i>Chesapecten</i> ^{a, b}	11.5 ± 2.1 (5)		27.7 ± 1.7 (5)	
		Morgarts Beach	<i>Carolinapecten</i> ^a		12.5		
		Rushmere	<i>Mercenaria</i> ^c	17 ± 1.8 (6)		26.2 ± 1.8 (6)	
			<i>Chesapecten</i> ^a		13.3		29.3
EPLI	Yorktown Formation (lower)	Sunken Meadow	<i>Chesapecten</i> ^a	11.4 ± 0.7 (3)		23.0 ± 1.0 (2)	
			<i>Placopecten</i> ^d	8.5 ± 0.9 (8)		17.3 ± 1.2 (8)	

Specimen code and source of $\delta^{18}\text{O}$ data (a, b, c)	Largest half-year increment (by $\delta^{18}\text{O}$)			Largest whole-year increment (by $\delta^{18}\text{O}$)		
	Height (mm)	Microgrowth increments		Height (mm)	Microgrowth increments	
		Number	Mean height (mm)		Number	Mean height (mm)
EPLI-GCP 1 ^a	37.5	153	0.245	47.5	187	0.255
EPLI-GCP 2 ^a	58.5	89	0.659	> 95.0	> 130	0.650
EPLI-MACP 1 ^a	54.5	> 18	1.163	57.0	> 21	1.146
EPLI-MACP 2 ^a	> 35.0	> 53	0.665	> 67.0	> 72	0.628
LPLI-GCP 1 ^b	106.0	> 94	0.718	> 128		
LPLI-GCP 2 ^a	> 48.5	> 38	0.841	> 68.5	> 166	0.786
LPLI-GCP 3 ^a	> 68.7	> 60	0.926			
LPLI-GCP 4 ^a	48.2	> 37	0.676	> 80.0		
LPLI-GCP 5 ^a	105.2	208	0.507	144.8	> 247	0.532
LPLI-GCP 6 ^a	121.7	164	0.743	145.7	223	0.655
LPLI-MACP 1 ^a	98.0	> 115	0.805	116.5	> 117	0.805
LPLI-MACP 2 ^a	> 51.5	> 58	0.699	> 62.5		
LPLI-MACP 3 ^a	> 50.5	> 61	0.823	> 74.5	> 74	0.799
LPLI-MACP 4 ^a	> 55.0	> 73	0.757	> 70.5	> 98	0.735
LPLI-MACP 5 ^a	42.1	> 30	0.761	> 63.5	> 69	0.655
LPLI-MACP 6 ^a	79.0	121	0.636	93.0	> 171	0.525
LPLI-MACP 7 ^c	> 20.0					
LPLI-MACP 8 ^c	> 34.0					
EPLI-GCP 1 ^a	73.7	151	0.491	126.8	> 211	0.517
EPLI-GCP 2 ^a	68.0	> 113	0.553	114.4	> 222	0.489
EPLI-MACP 1 ^a	> 33.0	> 54	0.416	> 52.6	> 119	0.353
EPLI-MACP 2 ^a	> 42.5	> 60	0.429	> 74.5	> 125	0.460
EPLI-MACP 3 ^c	> 30					
EPLI-MACP 4 ^c	25.0			42.0		
EPLI-MACP 5 ^c	> 29.0			> 46.0		
EPLI-MACP 6 ^c	16.0			26.0		
EPLI-MACP 7 ^c	> 47.0					
EPLI-MACP 8 ^c	25.0			43.0		
EPLI-MACP 9 ^c	23.0			40.0		
EPLI-MACP 10 ^c	24.0			41.0		
EPLI-MACP 11 ^c	25.0			> 45.0		
EPLI-MACP 12 ^c	24.0					

TABLE 2

TABLE 3

Specimen/division code; source of shell $\delta^{18}\text{O}$ data (a, b, c)	Temperature ($^{\circ}\text{C}$) for the preferred water $\delta^{18}\text{O}$		Temperature ($^{\circ}\text{C}$) for water $\delta^{18}\text{O} = +0.7\text{‰}$	
	Winter	Summer	Winter	Summer
EPLI-GCP 1 ^a	10.7	14.8	9.9	14.0
EPLI-GCP 2 ^a	12.5	21.4	11.7	20.5
EPLI-GCP mean	11.6 \pm 0.9	18.1 \pm 3.3	10.8 \pm 0.9	17.3 \pm 3.3
EPLI-MACP 1 ^a	9.8	21.3	9.8	21.3
EPLI-MACP 2 ^a	8.8	19.5	8.8	19.5
EPLI-MACP mean	9.3 \pm 0.5	20.4 \pm 0.9	9.3 \pm 0.5	20.4 \pm 0.9
LPLI-GCP 1 ^b	11.3	26.8	10.1	25.2
LPLI-GCP 2 ^a	13.8	24.7	12.5	23.2
LPLI-GCP 3 ^a	14.0		12.7	
LPLI-GCP 4 ^a	12.5	28.5	11.2	26.9
LPLI-GCP 5 ^a	7.2	21.6	6.1	20.1
LPLI-GCP 6 ^a	9.0	21.7	7.8	20.2
LPLI-GCP mean	11.3 \pm 2.5	24.7 \pm 2.7	10.1 \pm 2.4	23.1 \pm 2.7
LPLI-MACP 1 ^a	11.5	19.6	10.0	17.8
LPLI-MACP 2 ^a	5.6	21.4	4.2	19.6
LPLI-MACP 3 ^a	12.0	23.5	10.4	21.6
LPLI-MACP 4 ^a	12.4	23.3	10.8	21.4
LPLI-MACP 5 ^a	10.2	23.8	12.0	21.9
LPLI-MACP 6 ^a	9.8	21.7	8.3	19.9
LPLI-MACP 7 ^c	12.5	18.8	10.9	17.1
LPLI-MACP 8 ^c	14.5	26.8	12.9	24.8
LPLI-MACP mean	11.1 \pm 2.5	22.4 \pm 2.4	9.9 \pm 2.4	20.5 \pm 2.3
EPLI-GCP 1 ^a	11.9	26.0	14.7	29.5
EPLI-GCP 2 ^a	10.0	18.0	12.7	21.2
EPLI-GCP mean	11.0 \pm 1.0	22.0 \pm 4.0	13.7 \pm 1.0	25.4 \pm 4.2
EPLI-MACP 1 ^a	4.4	16.8	6.9	19.9
EPLI-MACP 2 ^a	6.1	19.2	8.7	22.4
EPLI-MACP 3 ^c	6.4	17.9	8.9	21.1
EPLI-MACP 4 ^c	5.7	17.9	8.2	21.1
EPLI-MACP 5 ^c	6.4	19.7	8.9	22.9
EPLI-MACP 6 ^c	6.4	22.0	8.9	25.3
EPLI-MACP 7 ^c	6.7	22.9	9.3	26.3
EPLI-MACP 8 ^c	9.3	22.0	12.1	25.3
EPLI-MACP 9 ^c	9.7	21.5	12.5	24.8
EPLI-MACP 10 ^c	9.3	22.5	12.1	25.8
EPLI-MACP 11 ^c	7.5	20.2	10.1	23.4
EPLI-MACP 12 ^c	5.7	19.3	8.2	22.5
EPLI-MACP mean	7.0 \pm 1.6	20.2 \pm 1.9	9.6 \pm 1.7	23.4 \pm 2.0