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

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

INTRODUCTION

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

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

As a contribution to debate over the cause of Plio-Pleistocene extinctions among marine bivalves in the eastern US, we present in this paper an investigation into the roles of declines in temperature and primary production in the extinction of a single species, the scallop (pectinid) *Carolinapecten eboreus* (Conrad, 1833). This species has a typical pectinid form but reaches an unusually large size (Fig. 1A), specimens up to 165 mm in height being known. Jones and Allmon (1995, fig. 10) obtained a long-wavelength ontogenetic profile of δ^{18}O from a large Florida Pliocene specimen. According to the standard interpretation of ontogenetic δ^{18}O profiles as signatures of seasonal temperature change, such long wavelength implies very rapid growth, which might have been a product of the high primary production indicated by other evidence (Allmon 1993; Allmon et al. 1995, 1996). We evaluate this possibility, and the question of whether decline in food supply rather than temperature led to the extinction of *C. eboreus*, through a wider investigation of growth rate in the species under circumstances of differing production and temperature. We use the associated fauna as an indicator of production and supply new estimates of temperature from shell δ^{18}O, also employing the seasonal fluctuation in this parameter as a time-marker to determine growth rate. We use shell δ^{13}C and the number and size of microgrowth increments (Fig. 1E, 1F) as supplementary indicators of production and growth rate, respectively.

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