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Response of a benthic suspension feeder (*Crassostrea virginica* Gmelin) to three centuries of anthropogenic eutrophication in Chesapeake Bay

Michael X. Kirby[a,*], Henry M. Miller[b]

[a]*Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA*
[b]*Historic St. Mary's City, P.O. Box 39, St. Mary's City, MD 20686, USA*

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Abstract

Biogenic reefs built by oysters and other suspension feeders are vital components of estuarine ecosystems. By consuming phytoplankton, suspension feeders act to suppress accumulation of organic matter in the water column. Nutrient loading increases the rate of primary production, thereby causing eutrophication. As suspension feeders consume more organic matter from increasing abundance of phytoplankton, their rate of growth should also increase if they are food limited. We show here that the eastern oyster, *Crassostrea virginica* (Gmelin), from St. Mary's and Patuxent rivers, Chesapeake Bay, grew faster during anthropogenic eutrophication relative to *C. virginica* before eutrophication. Growth of shell height, shell thickness and adductor muscle increased after eutrophication began in the late 18th century. After 1860, growth decreased, perhaps reflecting the negative effects of hypoxia, harmful algal blooms, disease and fishing on oyster growth. These results are consistent with the view that an increasing supply of phytoplankton resulting from eutrophication enhanced growth of *C. virginica* between 1760 and 1860, before oyster reefs were degraded by destructive fishing practices between 1870 and 1930. Alternative factors, such as changes in water temperature, salinity, and fishing are less likely to be responsible for this pattern. These results have implications for restoration of oyster reefs in order to mitigate the effects of eutrophication in estuaries, as well as the paleoecological relationship between suspension feeders and paleoproductivity.
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Keywords: eutrophication; paleoproductivity; growth rate; bivalve mollusc; oyster; *Crassostrea virginica*; Chesapeake Bay

1. Introduction

Eutrophication in Chesapeake Bay began in the late 18th century as a result of an increasing nutrient load from widespread deforestation associated with European agricultural practices (Cooper and Brush, 1991; Zimmerman and Canuel, 2002; Colman and Bratton, 2003). Yet, system-wide environmental deterioration did not become apparent until the early 20th century, almost 150 years after eutrophication started (Cooper and Brush, 1991; Adelson et al., 2001; Zimmerman and Canuel, 2002). Chesapeake Bay once had extensive biogenic reefs containing large populations of the eastern oyster *Crassostrea virginica* (Gmelin), as well as sponges, ascidians, barnacles and other suspension feeders (Winslow, 1880, 1882). Although these reefs began to form in the early Holocene after deglaciation and rise in sea level (Hargis, 1999), they were recently degraded and populations of *C. virginica* reduced through destructive fishing practices, particularly from bottom dredging between 1870 and 1930 (Rothschild et al., 1994). Before

* Corresponding author. Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Box 2072, Balboa, Panama.
E-mail address: kirbym@si.edu (M.X. Kirby).

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loss of biogenic reefs, did benthic suspension feeders remove increased organic matter resulting from eutrophication, thereby suppressing environmental deterioration for 150 years (Newell, 1988; Jackson et al., 2001)?

Eutrophication is an increase in the rate of primary production in an ecosystem (Nixon, 1995) and today is primarily a result of nutrient loading from anthropogenic sources, especially inputs of nitrogen and phosphorus compounds from agricultural fertilizers, urban sewage, animal waste and atmospheric fallout (Nixon, 1995; Bricker et al., 1997). Eutrophication is commonly associated with environmental deterioration, which is expressed as seasonal loss of dissolved oxygen, increased turbidity from increasing abundance of phytoplankton, loss of submerged aquatic vegetation, increased incidence of harmful algal blooms and an increase in parasitic diseases (Orth and Moore, 1983; Officer et al., 1984; Smayda, 1990; Burkholder et al., 1992; Bricker et al., 1997; Cloern, 2001). These phenomena are symptomatic of a major shift in trophic structure from a metazoan-based food web in which primary production is consumed mainly by suspension feeders, to a microbially dominated system in which primary production is mostly consumed by expanded populations of bacteria (Jonas, 1997; Jackson et al., 2001). It is necessary to differentiate between eutrophication and environmental deterioration because some estuaries may have eutrophication with little apparent environmental deterioration (Cloern, 1982; Officer et al., 1982; Stanley, 1992).

Suspension-feeding bivalves, such as *Crassostrea*, grow faster when access to their food supply increases (Malouf and Breese, 1977; Brown, 1988; Brown and Hartwick, 1988; Lenihan et al., 1996; Lenihan, 1999). The primary food source for *Crassostrea virginica* is phytoplankton (Langdon and Newell, 1996), which is the main group of primary producers that increases in abundance during eutrophication (Nixon, 1995). As eutrophication occurs, phytoplankton blooms increase in both size and frequency, thereby increasing the food supply to benthic suspension feeders. As suspension feeders consume this increasing supply of food, their rate of growth should also increase.

Our purpose is to test the hypothesis that an increasing rate of planktonic primary production will increase the rate of growth in suspension feeders. We specifically test the prediction from this hypothesis that an increasing supply of phytoplankton resulting from anthropogenic eutrophication enhanced the growth of *Crassostrea virginica* in Chesapeake Bay. A combination of paleoecological and archaeological data from the mesohaline section of Chesapeake Bay permits a test of this prediction. Archaeological and recent samples of 1695 shells collected from 24 sites in the St. Mary's and Patuxent rivers are used to construct a time series of growth rates that starts 500 years before the present, thereby encompassing the period of anthropogenic eutrophication (1760–2000), as well as providing a baseline before its start. Previously published analyses of sediment cores provide paleoenvironmental data that show the history of eutrophication. If growth rates were significantly higher during eutrophication relative to growth rates before, then these data would suggest that *C. virginica* consumed more organic matter resulting from eutrophication than before. However, when eutrophication is associated with environmental deterioration, then negative factors such as hypoxia and disease may act to decrease growth.

2. Material and methods

We limited our sampling to two tributaries of Chesapeake Bay: St. Mary's and Patuxent rivers, in order to control for geographic differences in temperature, salinity and other environmental factors that may affect growth rates (Fig. 1). Both areas offer collections of colonial to modern samples excavated from archaeological sites. Eleven samples containing a total of 977 *Crassostrea virginica* were collected from a small geographic area centered around St. Mary's City (38.1867°N, 76.4348°W). Thirteen samples containing a total of 718 *C. virginica* were collected from the lower Patuxent River (Fig. 1). All samples were derived from sealed deposits in pits, cellars, moats, or middens that displayed little to no evidence of disturbance since original deposition. A sealed horizon represents a stratigraphic layer that contains no post-depositional disturbance, indicating that younger artifacts are unlikely to have been mixed with older shells. Therefore, artifacts directly associated with shells in the same horizon are interpreted to be contemporaneous. These domestic (household) deposits contained artifacts mixed with animal bones and oyster shells from food consumption. Sample ages were determined through traditional methods of archaeological analysis (Noel Hume, 1969; Nash, 2000), which relies upon temporally diagnostic artifacts found in direct association with the shells (Rowe, 1962). In addition, documentary evidence is available for these historic-period sites that further constrains age dating (Miller, 1986). For example, sample ages are constrained by ceramics, tobacco pipes, glassware and other breakable artifacts that have known manufacturing periods (Noel Hume, 1969). Historical archaeological analysis indicates that these deposits were created over relatively brief periods, approximately of a decade or less. Standard analytic methods were applied to determine that these samples were from sealed horizons without significant post-depositional disturbance (Rowe, 1962; Noel Hume, 1969; Nash, 2000). Two prehistoric samples of *C. virginica* were dated by AMS ^{14}C analysis. In addition to the

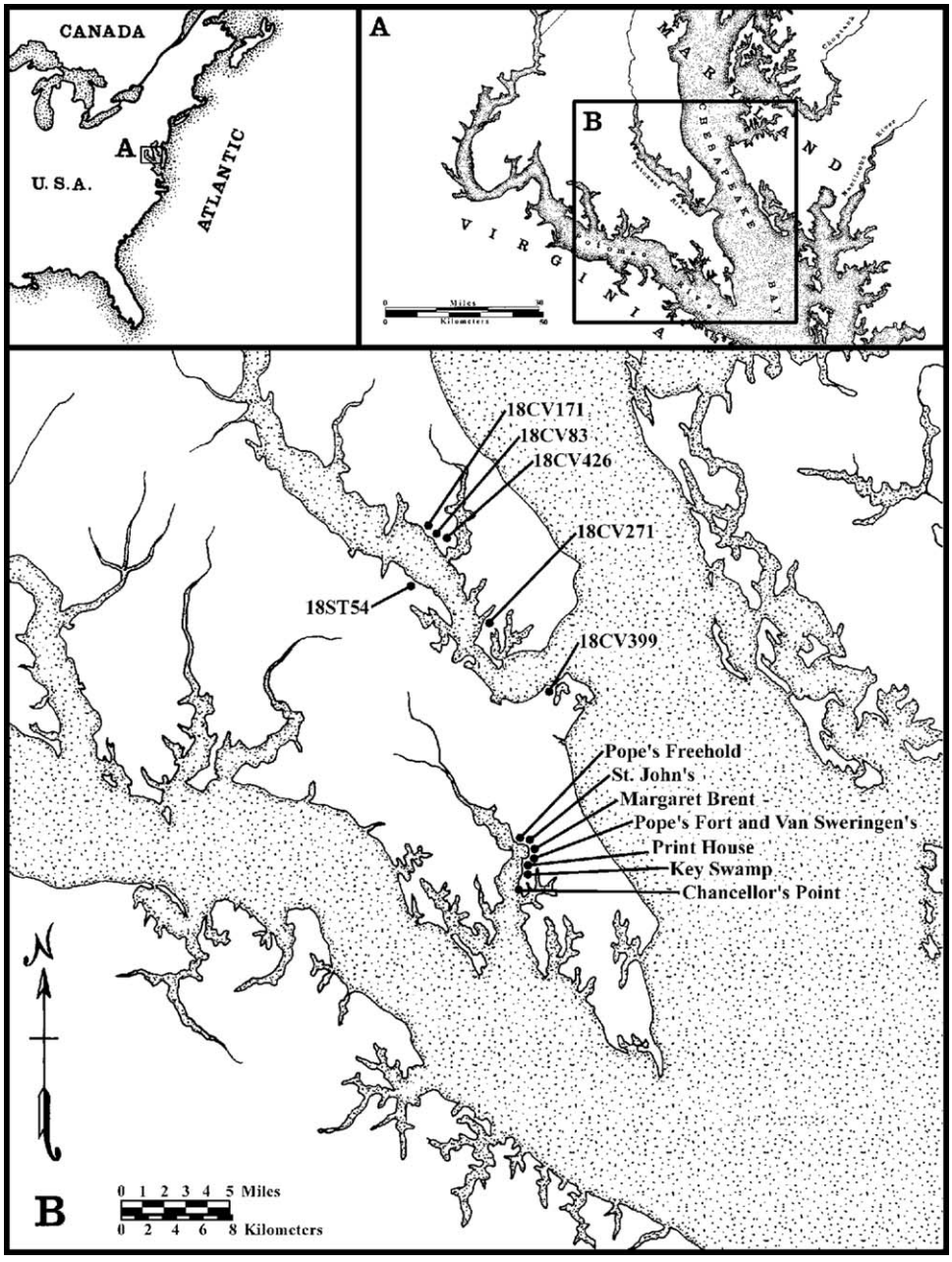

Fig. 1. Map of St. Mary's and Patuxent rivers, Chesapeake Bay, showing the location of archaeological and recent samples of *Crassostrea virginica* used in this study.

archaeological samples, we also used two recently collected samples of *C. virginica*: one collected on October 14, 2000, from the intertidal zone at Chancellor's Point, St. Mary's River, and the other collected in 1977 from Solomons Island, Patuxent River.

Shells of *Crassostrea virginica* were used because this species was the major suspension feeder in Chesapeake Bay (Newell, 1988) and should, therefore, have been sensitive to changes in primary production through time. Shells of *C. virginica* are also commonly found at archaeological sites in Chesapeake Bay. Two metrics were used to infer changes in shell growth of individual oysters (shell height and thickness); whereas a third metric (surface area of the adductor-muscle scar) was used to infer changes in growth of soft tissue, specifically the adductor muscle. We measured shell height as the longest dimension of the left valve and shell thickness at the ventral margin of the muscle scar with dial calipers (Kirby, 2001). Surface area of the adductor-muscle scar was measured with a visual-analysis computer program (NIH Image 1.62) from a scanned image of each muscle scar. We estimated life span by counting the number of annual ligamental increments in each left valve. Left valves of *C. virginica* commonly contain periodic

increments delineated by convex bands in the ligamental area that form annually (Kirby et al., 1998; Kirby, 2000). Growth rates were calculated from these measurements of the final size at death and estimated life spans. Kruskal–Wallis tests were used to test whether growth rates differed significantly between stages (Sokal and Rohlf, 1995). We used this non-parametric test because the data did not meet the assumption of homogeneity of variances. Where this test found a significant difference, we also employed the Scheffe's F procedure in order to determine which means were different from each other. This multiple comparison test is robust with samples having unequal sizes, heterogeneous variances and non-normality (SAS, 1999).

In addition to food supply, several other factors can affect the growth of *Crassostrea*, especially water temperature, salinity, depth, current flow, disease, fishing and genetic differences (Loosanoff and Nomejko, 1949; Ingle and Dawson, 1953; Galtsoff, 1964; Malouf and Breese, 1977; Brown, 1988; Brown and Hartwick, 1988; Lenihan et al., 1996; Shumway, 1996; Dittman et al., 1998; Lenihan and Peterson, 1998; Lenihan, 1999). In order to constrain these potentially confounding factors, we narrowed the geographic area of sampling to within 2 km of St. Mary's City for samples from St. Mary's River, and to the lowermost 25 km of the Patuxent River (Fig. 1). Based on historic evidence, it is likely that people collected *Crassostrea virginica* locally in these areas (Miller, 1986).

We divided the history of eutrophication in Chesapeake Bay into four stages in order to interpret past changes in growth of *Crassostrea virginica* relative to changes in primary production. The first stage (<1760) represents the interval before anthropogenic eutrophication and, therefore, represents the "natural" baseline for Chesapeake Bay. The second stage (1760–1860) encompasses the interval of eutrophication before system-wide environmental deterioration became apparent in direct observations of water quality (Sale and Skinner, 1917; Newcombe and Horne, 1938) or in sediment cores (Cooper and Brush, 1991; Adelson et al., 2001; Zimmerman and Canuel, 2002). Eutrophication began in the late 18th century as a result of widespread European agriculture and deforestation in the bay's watershed. At this time, farmers switched from a hoe-based, swidden type of farming to intensive plow agriculture (Walsh, 2001) that significantly increased sedimentation and nutrient loading to the bay (Brush, 1986). This historical event is recorded in sediment cores by a relative increase in ragweed pollen (*Ambrosia*) (Cooper and Brush, 1991). The third stage (1861–1920) represents a transitional interval between eutrophication without system-wide environmental deterioration and eutrophication with environmental deterioration. The fourth stage (>1920) represents the interval of eutrophication with clear evidence for system-wide environmental deterioration. Although boundaries between these four stages are approximate, they are apparent in paleoenvironmental analyses of sediment cores from the mesohaline section of Chesapeake Bay (Cooper and Brush, 1991; Zimmerman and Canuel, 2002; Colman and Bratton, 2003). We used data from Zimmerman and Canuel (2002) to construct two time series of the mass accumulation in the sediment of total organic carbon (TOC), which is a useful proxy for eutrophication, in order to compare changes in growth rate with eutrophication. These data were derived by Zimmerman and Canuel (2002) from two sediment cores taken from the mesohaline section of the main channel of Chesapeake Bay (cores RD [38.8867°N, 76.3917°W] and M3 [38.7183°N, 76.4467°W]).

3. Results

We analyzed 24 samples containing 1695 left valves of *Crassostrea virginica* from St. Mary's and Patuxent rivers (Table 1). Results from both rivers are consistent in showing that *C. virginica* grew faster in shell and soft tissue during the initiation of eutrophication in stage 2 (1760–1860) relative to *C. virginica* not yet exposed to eutrophication in stage 1 (1500–1759) (Table 2). Mean growth of shell height, shell thickness and muscle-scar area varied significantly with stage in oysters from both rivers (Fig. 2; Kruskal–Wallis, $p < 0.0001$). Mean growth was faster in *C. virginica* from stage 2 than *C. virginica* from all other stages (Fig. 3; Scheffe's F, $p < 0.0001$). The data also show that growth slowed after stage 2 (1861–2000), even though eutrophication continued to occur in Chesapeake Bay. Mean growth in *C. virginica* from stage 1 was not significantly different with *C. virginica* from stage 3 (Fig. 3). Shell height and thickness growth rates of *C. virginica* from the Patuxent River was significantly lower in stage 4 (Fig. 3). The faster rate of growth in oysters from stage 2 is apparent when life span is constrained by plotting growth rate as a function of life span (Fig. 4). Mean total organic carbon increased significantly between all four stages (Fig. 2D; Table 2; Kruskal–Wallis, $p < 0.0001$). In particular, TOC increased significantly between stages 1 and 2 in sediment cores RD and M3 ($p = 0.004$ and $p = 0.0188$, respectively).

4. Discussion

4.1. Eutrophication and faster growth

Our study provides a test of the hypothesis that an increasing rate of planktonic primary production will increase the rate of growth in suspension feeders. If our results showed that growth did not increase between

Table 1
Locality and archaeological data for samples of *Crassostrea virginica* from Chesapeake Bay

River	Locality	Site	Provenience	*N*	Age range	Stage
St. Mary's	St. John's Privy	18ST1-23	53/55	79	1640–1655	1
St. Mary's	Pope's Fort	18ST1-13	1944P	174	1644–1655	1
St. Mary's	St. John's Pit	18ST1-23	50M/50P	30	1650–1665	1
St. Mary's	Chancellor's Point	18ST1-62	24E 25F 25H	114	1640–1680	1
St. Mary's	St. John's Large Pit	18ST1-23	10,10B,D,E,11	121	1680–1700	1
St. Mary's	Print House Pit	18ST1-14	1463R	148	1680–1700	1
St. Mary's	St. John's Cellar	18ST1-23	80D	49	1700–1725	1
St. Mary's	Margaret Brent Hall	18ST1-110	2724J	53	1760–1780	2
St. Mary's	Pope's Freehold	18ST2	–	30	1820–1860	2
St. Mary's	Key Swamp	18ST1-43A	–	115	1890–1915	3
St. Mary's	Chancellor's Point	–	–	64	2000	4
Patuxent	Cumberland F-1	18CV171	249 F1	126	1510–1640	1
Patuxent	Cumberland F-2	18CV171	249 F2	35	1510–1640	1
Patuxent	Patuxent Point 1914E	18CV271	1914E	97	1658–1670	1
Patuxent	Patuxent Point 1610K	18CV271	1610K	86	1680–1690	1
Patuxent	Patuxent Point 1710W	18CV271	1710W	72	1680–1690	1
Patuxent	Kings Reach 213S	18CV83	213S	37	1690–1730	1
Patuxent	Susquehanna 1317G	18ST399	1317G	29	1780–1830	2
Patuxent	Sotterley Plantation	18ST54	N7995 E8015	45	1830–1900	3
Patuxent	Susquehanna 1120H	18ST399	1120H	48	1850–1900	3
Patuxent	Susquehanna 1214E	18ST399	1214E	27	1850–1940	3
Patuxent	Sukeeks Cabin 4970B	18CV426	4970B	63	1873–1923	3
Patuxent	Sukeeks Cabin 5069B	18CV426	5069B	25	1873–1923	3
Patuxent	Solomons	–	–	28	1977	4

stages 1 and 2 when primary production was increasing in the absence of the negative effects of environmental deterioration, then we would have rejected this hypothesis. As our results are consistent with this hypothesis, we infer that growth rate may be an appropriate proxy for inferring past changes in primary production (except when associated with environmental deterioration; see below). Furthermore, these results are consistent with the biogeographic hypothesis put forward by Vermeij (1978, p. 157) that larger adult size in molluscs in areas of high planktonic productivity results from faster growth rates during their active growth phase. Although previous studies have shown infaunal bivalves growing faster under recent eutrophication (Cederwall and Elmgren, 1980; Beukema and Cadée, 1986, 1991; Beukema et al., 2002), our study is the first to show epifaunal bivalves growing faster under historical eutrophication starting centuries ago. These results have implications to studies examining the paleoecological relationship between suspension feeders and planktonic primary production through the Phanerozoic (Vermeij, 1978, 1987, 1995; Jones and Allmon, 1995; Roopnarine, 1996; Eliuk, 1998; Kirby, 2000, 2001; Steuber, 2000; Allmon, 2001; Anderson, 2001; Teusch et al., 2002; Todd et al., 2002).

Faster growth during the initiation of eutrophication, but not after system-wide environmental deterioration, also has implications for previous studies that have

Table 2
Mean stage data for St. Mary's and Patuxent rivers

Parameter	Stage 1 (<1760)	Stage 2 (1760–1860)	Stage 3 (1861–1920)	Stage 4 (>1920)
St. Mary's River				
Growth rate of shell height (mm/yr)	25.3 ± 10.2	37.3 ± 18.5	20.0 ± 6.8	24.8 ± 7.9
Growth rate of shell thickness (mm/yr)	1.7 ± 0.84	2.4 ± 1.3	1.4 ± 0.51	1.5 ± 0.66
Growth rate of adductor muscle (mm^2/yr)	0.49 ± 0.27	0.76 ± 0.38	0.43 ± 0.19	0.49 ± 0.18
Patuxent River				
Growth rate of shell height (mm/yr)	23.5 ± 9.3	34.3 ± 14.4	24.1 ± 8.7	16.9 ± 3.3
Growth rate of shell thickness (mm/yr)	1.7 ± 0.66	2.5 ± 1.2	1.7 ± 0.65	1.2 ± 0.36
Growth rate of adductor muscle (mm^2/yr)	0.58 ± 0.27	0.86 ± 0.35	0.66 ± 0.28	0.53 ± 0.13
Chesapeake Bay				
Total organic carbon (mg/cm^2/yr) (RD)	6.3 ± 1.1	9.1 ± 1.7	18.5 ± 4.7	32.1 ± 4.7
Total organic carbon (mg/cm^2/yr) (M3)	3.7 ± 0.3	4.8 ± 0.4	6.4 ± 1.6	13.6 ± 2.7

Reported as mean ± one standard deviation.

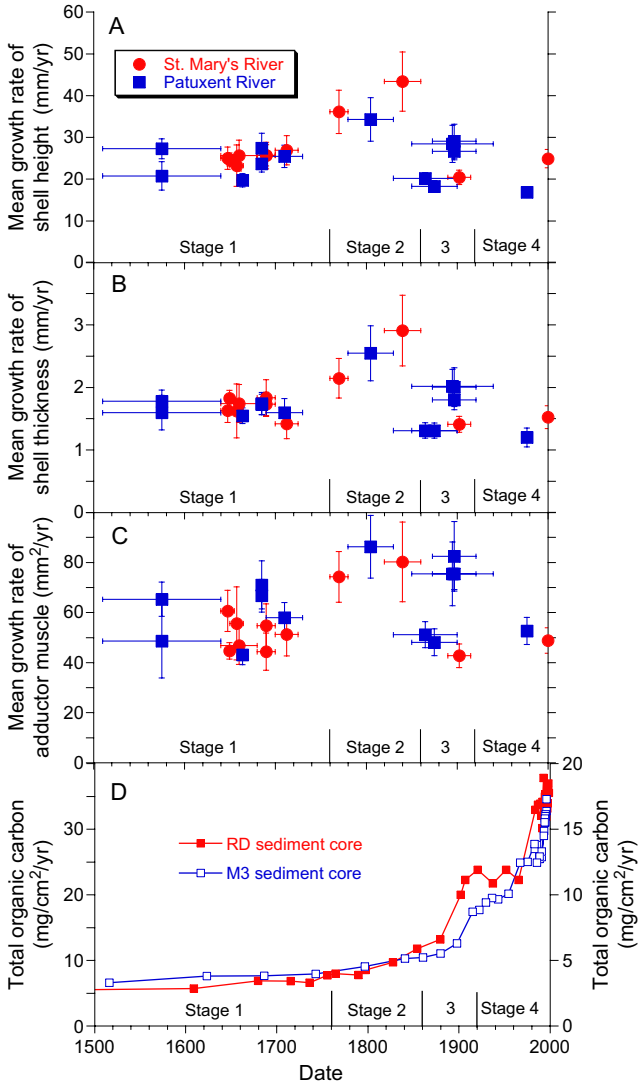

Fig. 2. Scatter plots showing mean growth rate of *Crassostrea virginica* from the St. Mary's and Patuxent rivers and total organic carbon from two sediment cores as a function of time (stage). (A) Mean growth rate of shell height. (B) Mean growth rate of shell thickness. (C) Mean growth rate of adductor muscle. (D) Mass accumulation of total organic carbon derived from two sediment cores taken from the mesohaline section of the main channel of Chesapeake Bay (cores RD [38.8867°N, 76.3917°W] and M3 [38.7183°N, 76.4467°W]; data from Zimmerman and Canuel, 2002; core RD = left *y*-axis). History of eutrophication is subdivided into four stages: (1) Before eutrophication (<1760); (2) eutrophication before system-wide environmental deterioration (1760–1860); (3) transitional interval between eutrophication without system-wide environmental deterioration and eutrophication with environmental deterioration (1861–1920); and (4) eutrophication with system-wide environmental deterioration (>1920). Horizontal error bars represent time ranges. Vertical error bars represent 95% confidence intervals.

suggested that benthic suspension feeders may suppress the effects of eutrophication by preventing the accumulation of organic matter in the water column (Officer et al., 1982; Newell, 1988; Jackson et al., 2001). These studies suggested that without this top–down control on phytoplankton, organic matter would instead be decomposed by expanding populations of bacteria that deplete dissolved oxygen in the water column, thereby causing hypoxia (<4 mg O_2/L) and other environmental problems (Jonas, 1997). Our results are consistent with this model of suspension feeders as top–down controllers of planktonic production. By showing that both shell and soft-tissue growth increased significantly during eutrophication, we infer that a percentage of the increased primary production resulting from eutrophication was consumed by *Crassostrea virginica* in St. Mary's and Patuxent rivers and converted into oyster biomass. By removing increased primary production from the water column, *C. virginica* made this organic matter accessible to other metazoans, specifically their predators, which was then exported up the food web. Hence, levels of biofiltration, reef production and production of reef-associated organisms such as fish, may all be expected to have increased as well. Changes in one or more of these would have far reaching implications for the estuarine ecosystem in Chesapeake Bay. Alternatively, without *C. virginica* or other suspension feeders available, the organic matter from eutrophication would instead most likely have been consumed by microbial populations during stage 2. The start of environmental deterioration in the late 19th to early 20th centuries coincided with overfishing and physical degradation of oyster reefs primarily through bottom dredging for *C. virginica* in the open channels of Chesapeake Bay between 1870 and 1930 (Rothschild et al., 1994). The coincidence between environmental deterioration, degradation of oyster reefs and the decrease in growth of intertidal oysters reported here, suggests that these events may have been interrelated.

4.2. Alternative factors for faster growth

In addition to changes in primary production resulting from anthropogenic eutrophication, there are other factors that also need to be considered, particularly changes in water temperature and salinity, that can potentially affect growth rate (Ingle and Dawson, 1953; Remane and Schlieper, 1971). Although there is evidence that both temperature and salinity changed slightly over the last five centuries (Cronin et al., 2000, 2003), these changes are relatively small compared to the huge change in primary production over the past three centuries (Zimmerman and Canuel, 2002; Colman and Bratton, 2003). We, therefore, think it unlikely that these alternative factors had as strong an effect as eutrophication, which increased dramatically the rate of primary production 2.5 times over the past three centuries (Zimmerman and Canuel, 2002).

Fishing may also affect growth by decreasing intraspecific competition for primary production or space for

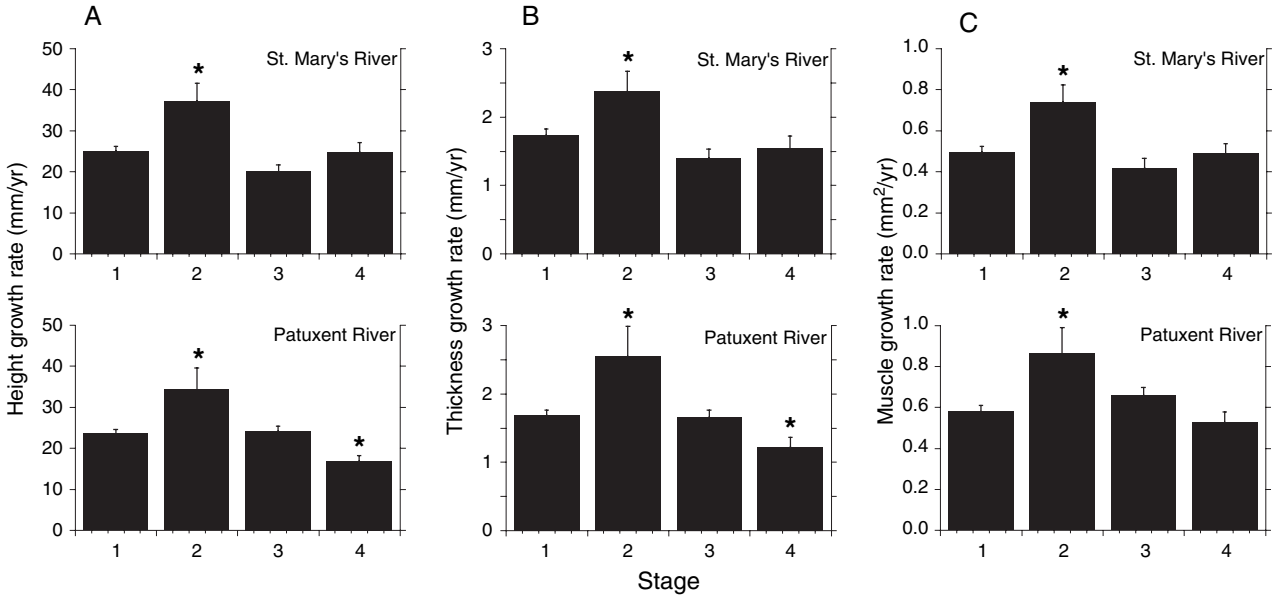

Fig. 3. Bar graphs showing mean growth rate of *Crassostrea virginica* from St. Mary's and Patuxent rivers as a function of time (stage). (A) Mean growth rate of shell height. (B) Mean growth rate of shell thickness. (C) Mean growth rate of adductor muscle. Vertical error bars represent 95% confidence intervals (* = Growth rate in stage is significantly different from all other stages at $\alpha = 0.01$ [Scheffe's *F*]).

shell growth. If fishing had removed large numbers of *Crassostrea virginica* from Chesapeake Bay, then we may expect surviving *C. virginica* to have grown faster because there would have been more primary production available. We are able to reject this alternative possibility for two reasons. First, stages 1 and 2 were before the period of overfishing, which occurred between 1870 and 1930 (Rothschild et al., 1994). Second, if earlier fishing had removed enough *C. virginica* to have affected the levels of primary production that was left unconsumed in the water column, thereby allowing surviving *C. virginica* to grow faster, then this would also have resulted in eutrophication (Nixon, 1995). We may not be able to distinguish between eutrophication resulting from an increased nutrient load or from fewer suspension feeders, but we can infer the impact on growth of *C. virginica* resulting from relative changes in primary production.

Related to the potential impact of fishing is the question of whether or not oysters were food limited before overfishing degraded their reefs. Today, oysters are not food limited in Chesapeake Bay. Living oysters may have problems, but access to food is not one of them (unless it is the replacement of preferred diatoms with less preferred dinoflagellates and cyanobacteria). But three centuries ago, when historical accounts indicate that the clarity of the water column was such that the bottom of Chesapeake Bay was visible through 10 m of water, there probably was greater competition among suspension feeders for phytoplankton. We may never be able to determine how food-limited oysters were before reef degradation, but it is a mistake to ignore the shifting baseline syndrome (Pauly, 1995) and assume that the past was like today.

4.3. Environmental deterioration and slower growth

Slower growth in stages 3 and 4 relative to stage two suggests that other factors counteracted the potential benefits gained from positive factors, such as an increasing food supply in the late 19th–20th centuries. The main difference in Chesapeake Bay after stage two (>1860) is the rise of system-wide environmental deterioration near the start of the 20th century (Cooper and Brush, 1991; Adelson et al., 2001; Zimmerman and Canuel, 2002; Colman and Bratton, 2003). There are many factors associated with environmental deterioration that are known to negatively affect the fitness and growth of *Crassostrea virginica* (Galtsoff, 1964; Ford and Tripp, 1996; Lenihan and Peterson, 1998; Lenihan et al., 1999). The most important factors include seasonal loss of dissolved oxygen (hypoxia), increased blooms of harmful algae, increased incidence of parasitic disease and habitat disturbance due to fishing. Most of these phenomena are symptomatic of a major shift in trophic structure from a metazoan-based food web in which primary production is grazed by benthic suspension feeders, to a microbially dominated system in which primary production is mostly consumed by expanded populations of bacteria (Jonas, 1997; Jackson et al., 2001). Although there are perhaps hundreds of factors that may cause oysters to grow slower, we consider below the potential for those factors that we think most likely to have affected growth rates of *C.*

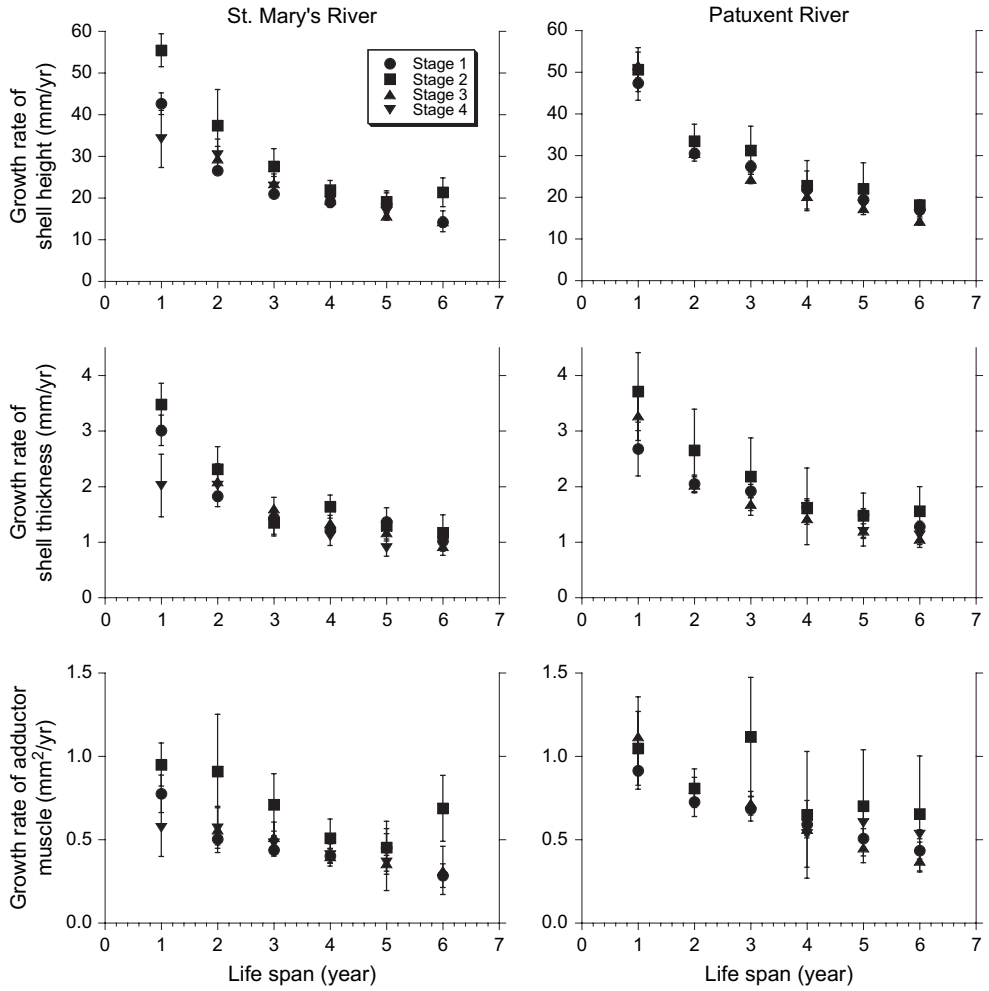

Fig. 4. Scatter plots showing mean growth rate of *Crassostrea virginica* from St. Mary's and Patuxent rivers plotted as a function of life span. Growth rate decreased with increasing life span. Note that growth rates through the ontogeny of stage 2 oysters are higher than growth rates of oysters in all other stages, with the greatest difference commonly between stages 1 and 2. Vertical error bars represent 95% confidence intervals.

virginica from both the St. Mary's and Patuxent rivers after 1860.

Hypoxia (<4 mg O_2/L) occurs when organic matter accumulates in the water column or on the seafloor where it may undergo microbial decomposition that depletes the available dissolved oxygen (Officer et al., 1984; Paerl et al., 1998). Hypoxia generally has a detrimental effect on benthic biota (Officer et al., 1984; Malone et al., 1986) and has specifically been shown to decrease fitness in recent *Crassostrea virginica* from Pamlico Sound (Lenihan and Peterson, 1998). It is possible that seasonal hypoxia had a detrimental effect on our samples as early as the beginning of the 20th century. The earliest published observations of hypoxia in Chesapeake Bay are from the Potomac River in 1912, close to St. Mary's River (Sale and Skinner, 1917). Hypoxia was again observed in 1936, this time in the Patuxent River and main channel of the bay (Newcombe and Horne, 1938). These observations are consistent with paleoenvironmental evidence from sediment cores that shows increasing hypoxia in the early 20th century (Cooper and Brush, 1991; Adelson et al., 2001; Zimmerman and Canuel, 2002). Hypoxia is commonly a function of stratified water in which denser bottom water is depleted in oxygen relative to less dense but oxygenated surface water (Officer et al., 1984). Intertidal biota, such as our samples, may, therefore, be safe from underlying hypoxia most of the time. Malone et al. (1986), however, have shown that hypoxia can reach the surface in Chesapeake Bay on occasions. They observed dead and moribund crabs, fish and birds in an area where hypoxia had invaded the intertidal zone of the western flank of Chesapeake Bay. Although these observations are circumstantial, they do show that the start of widespread hypoxia coincided with lower growth rates observed in stages 3 and 4.

Harmful algal blooms can also decrease the fitness of *Crassostrea virginica* because harmful algae, such as some dinoflagellates and cyanobacteria, are either of less nutritional value than diatoms, which are known to be

preferred by *Crassostrea* species (Langdon and Newell, 1996), or harmful algae secrete toxic substances that are detrimental to oysters (Loosanoff and Engle, 1947). Both laboratory (Loosanoff and Engle, 1947) and field observations (Galtsoff, 1964) have shown that harmful algae or their blooms can have a deleterious effect on *C. virginica*. Evidence from lipid biomarkers preserved in sediment cores demonstrates that the abundance of dinoflagellates and cyanobacteria relative to diatoms has increased in the 20th century in Chesapeake Bay (Zimmerman and Canuel, 2002). This apparent change in planktonic-community structure from diatoms to dinoflagellates/cyanobacteria may have negatively affected the growth of *C. virginica* during stages 3 and 4.

A number of diseases have a deleterious effect on *Crassostrea virginica* (Galtsoff, 1964; Ford and Tripp, 1996; Lenihan et al., 1999). These diseases are primarily caused by protistan parasites, specifically *Perkinsus marinus* (Dermo disease), *Haplosporidium nelsoni* (MSX disease) and *Haplosporidium costale* (SSO disease) (Ford and Tripp, 1996). These parasites can chronically weaken and eventually kill *C. virginica* over a period of years (Ford and Tripp, 1996; Lenihan et al., 1999). Only the later samples in stage 4 were likely to have been exposed to these parasites, because in Chesapeake Bay, Dermo was first observed in 1949 and MSX and SSO in 1959 (Andrews and Hewatt, 1957; Wood and Andrews, 1962; Andrews, 1966). As these diseases only became common in the last half of the 20th century in Chesapeake Bay (Andrews, 1996), it is unlikely that they could have affected *C. virginica* in samples from stage 3.

Lastly, habitat disturbance due to fishing has been shown to negatively affect growth in *Crassostrea virginica* (Lenihan and Peterson, 1998; Lenihan, 1999). There is abundant evidence that fishing for *C. virginica* intensified through the 19th and 20th centuries in Chesapeake Bay (Rothschild et al., 1994). Harvesting damage to reefs reduces growth through changes in hydrodynamics, sedimentation and disease (Lenihan and Peterson, 1998; Lenihan, 1999; Lenihan et al., 1999). It is possible that habitat disturbance from destructive fishing practices may have contributed to lower growth rates in our samples from St. Mary's and Patuxent rivers after 1860.

5. Conclusions

Paleoecological data derived from archaeological sites and sediment cores allow us to determine the response of a benthic suspension feeder to almost three centuries of anthropogenic eutrophication in Chesapeake Bay. The eastern oyster *Crassostrea virginica* from St. Mary's and Patuxent rivers grew significantly faster in both shell and soft tissue during eutrophication between 1760 and 1860. This is consistent with the hypothesis that an increasing supply of phytoplankton resulting from eutrophication should enhance growth of benthic suspension feeders. Slower growth rates between 1860 and 2000 may be a result of the negative effects of system-wide environmental deterioration from hypoxia, harmful algal blooms, disease and fishing disturbance that began to occur during this interval. This study shows how historical disciplines such as paleoecology and archaeology can contribute to understanding past ecological changes initiated by humans centuries ago.

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