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SHELL LENGTH-AT-AGE RELATIONSHIPS IN JAMES RIVER, VIRGINIA, OYSTERS (*CRASSOSTREA VIRGINICA*) COLLECTED FOUR CENTURIES APART

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ABSTRACT Eastern oysters were ecologically and structurally dominant features of the Chesapeake Bay prior to European colonization. Four centuries of harvest pressure, habitat degradation, and, more recently, disease activity have affected extant oyster population demographics. We compared population demographics and age-at-shell length relationships for modern mesohaline James River oyster populations with James River oysters collected in the years 1611 to 1612 by Jamestown settlers. Historic oyster collections made by hand included a more complete demographic than modern samples collected with patent tongs. Historic oysters had significantly faster growth rates than modern oyster populations. Modern oysters larger than 30–40 mm SL or age 1 grow more slowly than historic oysters of comparable ages. Unlike historic oyster populations, modern James River oyster populations are affected by Dermo and MSX. The downward trend observed in the modern age at length relationship (Fig. 4B see later) between 1 to 1.6 y is probably related to the seasonal onset of disease with increasing temperatures. Observed changes in oyster demographics and growth rates across four centuries reflect changes in the environment as well as changes in oyster biology because of chronic pressure from two oyster diseases.

KEY WORDS: Eastern oyster, *Crassostrea virginica*, James River, age-at-length, Jamestown, Chesapeake Bay

INTRODUCTION

Eastern oysters dominated the shallow habitats of Chesapeake Bay as ecological service providers and habitat engineers prior to the 17th century (Baird & Ulanowicz 1989, Kennedy 1996). Since the 17th century, anthropogenic habitat modifications to the Chesapeake Bay including habitat destruction and removal as well as deterioration related to changes in system wide nutrient and sediment levels, fluxes, and pathways have combined with oyster population reductions because of fishing pressure and, since 1959, disease. Modern oyster populations have drastically changed from their original status in the Bay (Newell 1988, Rothschild et al. 1994, Woods et al. 2005), and these changes are concurrent with fundamental changes in ecosystem function (Newell 1988, Ulanowicz & Tuttle 1992).

Restoration efforts targeting the oyster resource make the assumption that adding more oysters or facilitating habitat development through shell planting will provide the basis for achieving demographic parity with the original populations. Inherent in this strategy is the assumption that the Chesapeake Bay habitat has not fundamentally changed and is equally suitable for oyster growth and success in the modern as it was pre-European colonization. The numerous and cumulative pressures placed on modern Chesapeake Bay estuaries from four centuries of ever increasing shoreline development, habitat fragmentation, declines in water quality, reduction in oyster density and presumably genetic diversity as well as challenges posed by two oyster diseases, Dermo (*Perkinsus marinus*) and MSX (*Haplosporidium nelsoni*), call this base assumption into question (Powell & Klinck 2007, Mann & Powell 2007).

We compare demographic based age at shell length (mm) relationships for James River, VA oysters collected in the years 1611 to 1612 and 2005 to 2008 to test the assumption that oyster growth rates in modern times are similar to growth rates pre-European colonization.

MATERIALS AND METHODS

Modern Salinity Data

Salinities (ppt) within 0.5 m of the bottom have been collected weekly at Wreck Shoal (Fig. 1) and one of three downriver sites (Thomas Rock, Brown Shoal, Miles Watch House [Fig. 1]) from June through September as part of the Virginia Institute of Marine Science (VIMS) Spatfall Monitoring program since the early 1980s. The three downriver sites are within close proximity to each other (Fig. 1), are of similar depths (2–3 m), and are considered as a single unit for descriptive purposes here. In March 2007, the VIMS Molluscan Ecology program established a year-round hydrographic monitoring station at Middle Ground in the lower James River (Fig. 1). This station records salinity (ppt) 0.25 m from the bottom at 15 min intervals.

Oyster Sources

Modern James River oyster populations at Brown Shoal/Thomas Rock (2006 to 2007), and Wreck Shoal (2005 to 2007; Fig. 1) were sampled as part of the annual fall (October or early November) VIMS/VMRC patent tong surveys for stock assessment. During the stock assessment, a hydraulic patent tong was used to sample 1 m² of subtidal bottom. Shell height, the maximum dimension from hinge to growth edge, is commonly referred to as shell length and shell length will be used to describe this dimension here. The shell length (mm) of every live oyster collected within each patent tong grab was measured to the nearest mm. Additional samples were collected from these three sites during May 2008 using a dredge (61 cm wide with 10 cm teeth). Shell length was also measured for live oysters sampled from each dredge tow to the nearest mm. Depth at all three of these sites was 2–4 m. These reefs are within the mesohaline (10–23 ppt) portion of the James River (Fig. 1, Fig. 2) and do not experience seasonal hypoxia or anoxia (Southworth, unpublished data).

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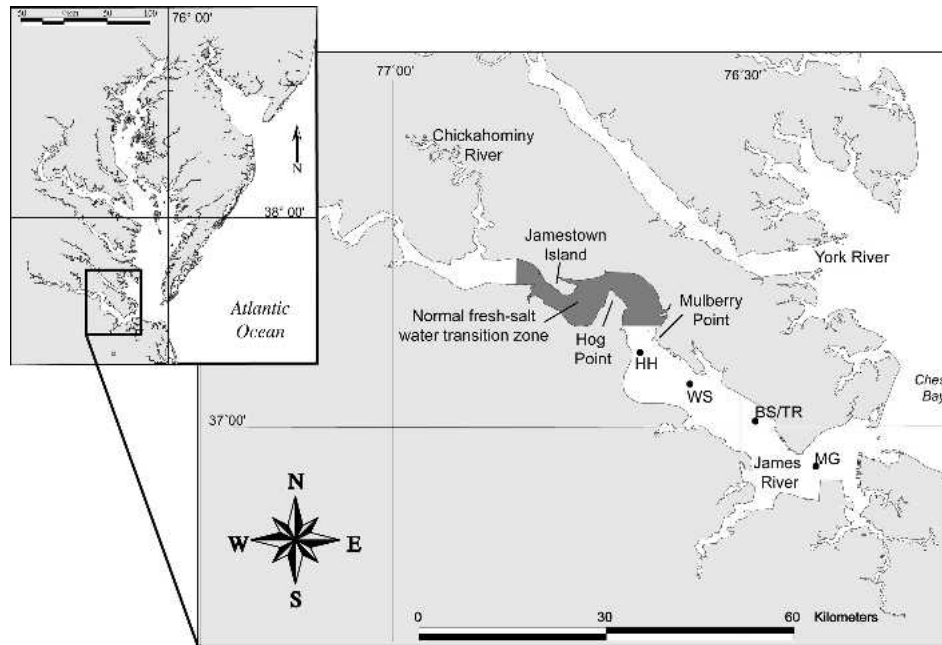


Figure 1. Map of James River showing oyster collection and hydrographic sites including Wreck Shoal (WS), Brown Shoal/Thomas Rock/Miles Watch House (BS/TR), Middle Ground (MG), and Horsehead (HH).

Oyster shells recovered from a well discovered by the Association for the Preservation of Virginia Antiquities archaeologists within the James Fort walls (= Jamestown) during spring 2006 (APVA ID = JR 2158) were examined. Jamestown

colonists relied on the James River oyster populations as a food source with the empty shells used as either building material or discarded as trash (Kelso & Straube 2004, Kelso 2006). Oyster harvesting by the colonists was typically done opportunistically by hand at low tide from intertidal oyster populations within the region between Jamestown Island and Hog Island/Mulberry Point (Fig. 1, Schmidt & Haven 2004). Thus, only oysters that were accessible, removable, and suitably sized for food were targeted by colonial collections. In fact, larger food-grade oyster shells were not always separated from spat or smaller oysters prior to opening and the archaeological shell deposits from this James Fort well contain oysters ranging from approximately 8 to >160 mm shell length.

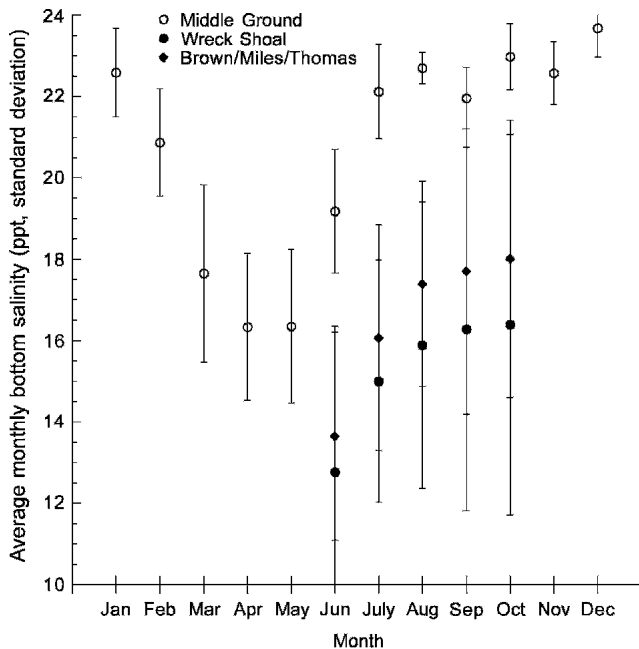


Figure 2. Annual salinity profile (average monthly bottom salinity (ppt) with standard deviation) for modern James River collection sites. Only months with more than twenty salinity measurements (typically June–October) are presented for Wreck Shoal (1982–1985 and 1989–2008) and Brown Shoal/Thomas Rock (1982–1997). Middle Ground data points are the average of >1,000 data points per month.

This James Fort well was in use for some period of time between the years 1611 and 1616. (W. Kelso, B. Straube, D. Schmidt, APVA, pers. comm.). It was abandoned, filled, and sealed by 1616 when a house foundation was built on top of it. There was no mixing of artifacts from within the well with later time periods below the surface contact layers including the plow zone. Whereas in use, the well would have received minor accidental input of artifacts. Abandoned wells were quickly filled, typically with trash including oyster shells (Kelso & Straube 2004, Kelso 2006). Thus oyster shells from this James Fort well are unique to the 1611 to 1616 time period (W. Kelso, B. Straube, D. Schmidt, APVA, pers. comm.). During the excavation process, archaeologists divided the well fill into coherent units or layers on the basis of artifacts and soil characters. Shell lengths (mm) of intact left oyster valves were measured from James Fort well layers P (collected in early summer [= May]) and Z (collected in winter [= December]).

Shell width (mm), the maximum dimension perpendicular to shell length, was measured for a subset of modern oysters and all James Fort oysters. Oysters grow isodiametrically and are plastic with regard to morphological form. Shell length to shell

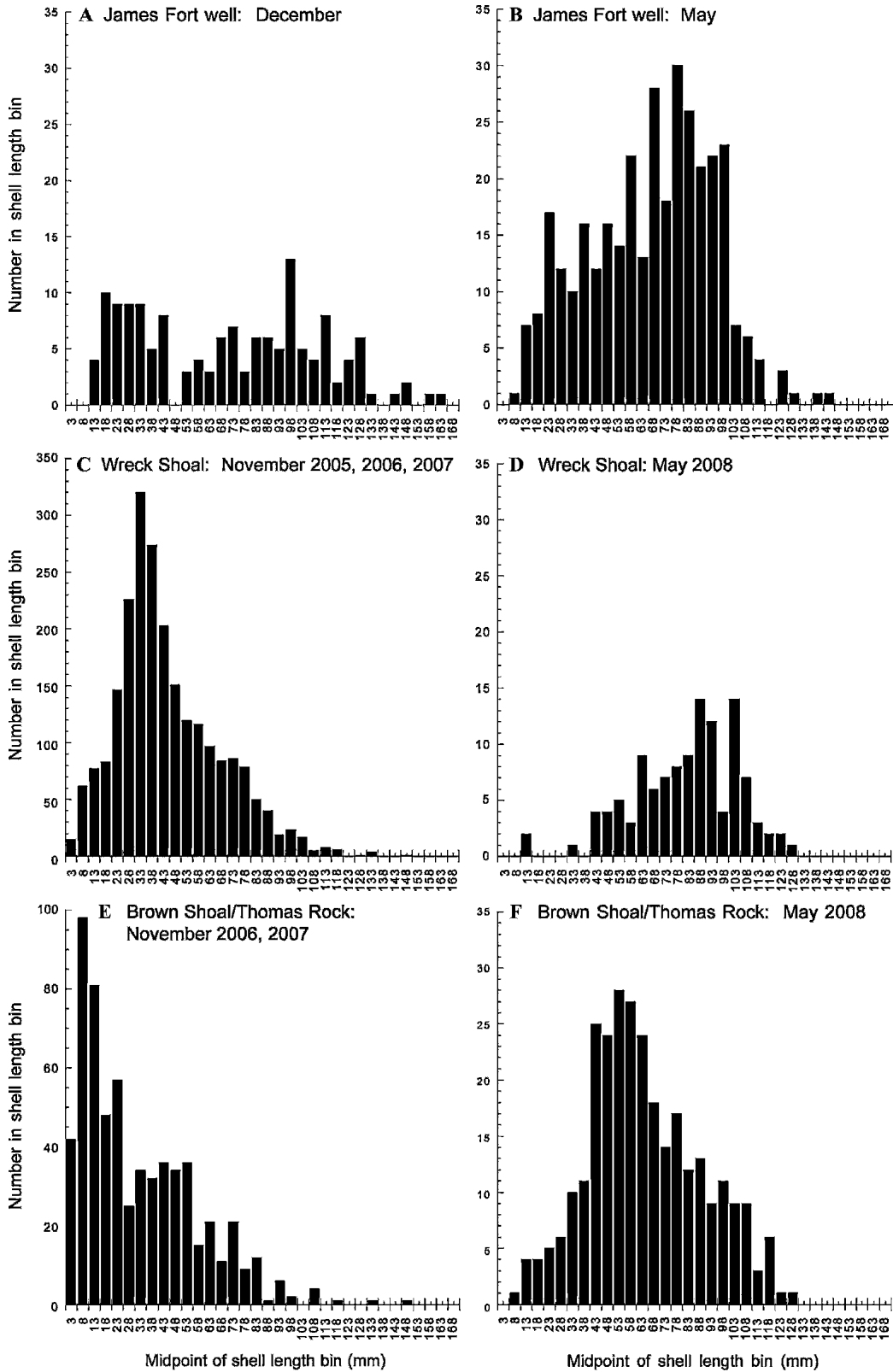


Figure 3. Length-frequency distributions for James Fort (A, $n = 145$; B, $n = 339$) and modern James River oyster (C, $n = 2312$; D, $n = 118$; E, $n = 628$; F, $n = 292$) populations.

width ratios can be used to characterize oyster morphological forms (Harding & Mann 2006, Harding 2007) and research is ongoing to describe the relationship of oyster morphology, density, and habitat type in the James River (Harding, Southworth, Mann, unpublished data). These analyses were restricted to modern and historic oysters with shell length to shell width ratios less than 1.9 to ensure that only similar growth forms were being compared.

Data Analyses

Length-frequency distributions using 5 mm bins were prepared for each modern reef and James Fort layers P and Z. The individual cohorts (not year classes, there being one or more cohorts in a single year class) within each distribution were identified by the method of Bhattacharya (1967). The range and modal length of each modern cohort was identified using long-term recruitment patterns developed from annual spatfall reports for the James River (Southworth et al. 2003–2008; available at <http://www.vims.edu/mollusc/publications/mepubamr.htm>) resulting in two or three identifiable cohorts per year. Historic populations were assumed to produce a minimum of two and a maximum of three cohorts per breeding season. We assumed a birth date of July 1, for all oysters. Ages were assigned as years including fractions of a year based on collection date. Ages of October, December, and May collections began at 0.33, 0.5, and 0.83 y, respectively. Cohorts were thus assigned to years and a linear age-at-length relationship (Shell length = $m \cdot \text{Age} + b$) was fit to the data. A linear fit is appropriate for these data given the life expectancy of an oyster (10–15 y in undisturbed populations, [Powell & Cummins 1985]), the absence of oysters >5 y in these collections and the absence of an asymptote in the observed trajectories. Linear regressions were compared between modern sites and between modern and historic populations using *t*-tests (Zar 1996). Significance levels were set at $\alpha = 0.05$ *a priori*.

RESULTS

Average monthly salinity from Middle Ground (Fig. 2) clearly shows the seasonal pattern of wet (March to May) and dry (June to January) months that is characteristic of the James River (Stroup & Lynn 1963). Both Wreck Shoal and Brown Shoal/Thomas Rock/Miles Watch House show similar trends during the summer months. Whereas there is inter and intra-annual variation between salinities at all three of these sites as

indicated by the error bars (Fig. 2), these sites fall within the salinity limits of 10–23 ppt characteristic of mesohaline habitats year round.

A total of 643 James Fort oysters ranging in SL from 8.3–174.5 mm SL were used in these analyses (Fig. 3A to B). Modern James River oyster collections yielded 3,315 oysters with shell lengths of 3–150 mm (Fig. 3C to F). Age-at-length relationships for modern oyster populations were statistically similar (Table 1, Fig. 4A, $P > 0.05$, *t*-test). Thus modern age-at-length data were combined across sites for comparison with historic age-at-length data. There was a significant difference between the age-at-length relationships in historic and modern oyster populations (Table 1, Fig. 4B, *t*-test, $P < 0.05$). Modern oysters larger than 30–40 mm SL or Age 1 grow more slowly than historic oysters of comparable ages.

DISCUSSION

Modern oyster growth rates observed in these James River populations are higher than those recorded by Mann and Evans (2004) for an upriver reef in the James River (Horsehead, Fig. 1) and by Kraeuter et al. (2007) for Delaware Bay populations. Kirby and Miller (2005) also report declines in modern oyster growth rates relative to pre-European colonization in oysters from the St. Marys and Patuxent Rivers, MD. Differences in methodology as well as geographic location (depth, salinity, disease levels) between this study and Kirby and Miller (2005) prevent direct comparison of the actual growth rates but the observed trends are similar.

The James Fort well oysters were alive during the severe regional drought of the years 1606 to 1612 that has been described independently using tree rings (bald cypress, Stahle et al. 1998), benthic foraminiferans in Chesapeake Bay sediment cores (Karlsen et al. 2000, Cronin et al. 2000), and pollen data from Chesapeake Bay sediment cores (Brush 2001). Cronin et al. (2000) suggest that severe regional droughts described by Stahle et al. (1998) in the years 1587 to 1589 and 1606 to 1612 time frames would have reduced discharge by 40% to 50% and increased regional salinities by 10–15 ppt relative to modern (1990 to 2000) recorded values (Cronin et al. 2000). Maximum dry season salinities of 8–10.9 ppt were recorded at Jamestown Island (Fig. 1) during the relatively dry (drought) years of 1966, 1970, and 1977 (Brooks & Fang 1983, VIMS Juvenile Fish and Crab survey, unpublished hydrographic data) at discharge levels of 500–1500 cfs for the James River at Richmond (USGS surface water data).

TABLE 1.

Summary of linear regressions (SL = $m \cdot \text{Age} + b$) used to describe age-at-length relationships for modern and historic James River oyster populations. Abbreviations are as follows: N = number of x, y data pairs used to calculate regression, SE = standard error of the mean, R^2 = coefficient of determination.

Regression ID	Age-at-length Relationship	N	m (SE)	b (SE)	R^2	Regression ID & Comparison/ <i>t</i> statistic	P value
1	Modern: Brown/Thomas Rock	16	22.64 (1.17)	10.52 (3.08)	0.96	1 v 2/ 0.79	>0.05
2	Modern: Wreck Shoal	15	20.91 (1.52)	22.2 (3.87)	0.94		
3	All modern combined	31	21.57 (1.11)	14.43 (2.86)	0.94	3 v 4/6.97	<0.05*
4	Historic	17	31.67 (1.84)	7.15 (3.75)	0.95		

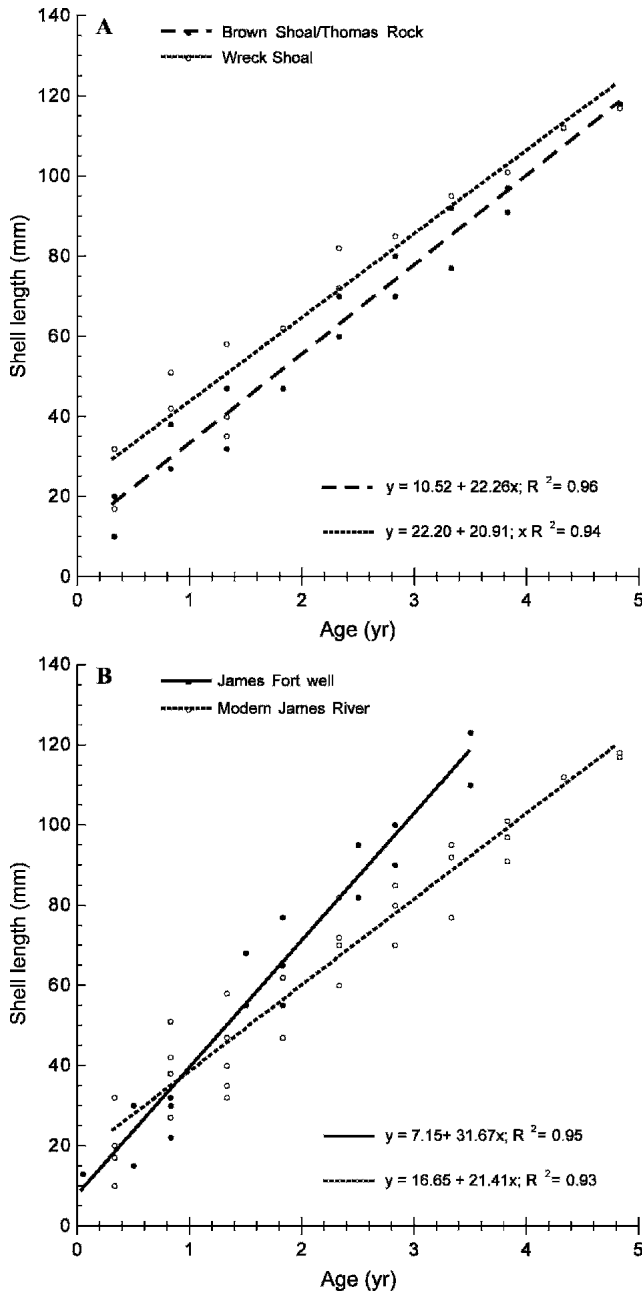


Figure 4. Age-at-shell length relationship for modern Brown Shoal/Thomas Rock and Wreck Shoal James River oyster populations (A) and both modern oyster populations in relation to historic oyster populations (B). Regression statistics are given in Table 1.

Discharge in the James River during a multiyear regional drought would have been as low as modern drought dry season discharge for most of the year and even lower during the normal dry season (June to October). Thus, salinities in the upper James River during the 1606 to 1612 drought would have been higher than modern salinities with the river reach from Hog Island to Jamestown Island (Fig. 1) maintaining mesohaline salinities year round caused by drought reduced discharge. All oysters examined here, modern oysters and historic oysters

that lived during the 1606 to 1612 drought, lived in mesohaline salinity conditions.

Unlike historic oyster populations, modern James River oyster populations are affected by Dermo and MSX. Both diseases have been present in the lower James River since 1959 (Andrews 1996). Dermo prevalence was 92% at Wreck Shoal and 100% at Thomas Rock in October 2005 (Carnegie & Burreson 2006). MSX prevalence was 20% at Wreck Shoal and 8% at Thomas Rock in October 2005 (Carnegie & Burreson 2006).

Both diseases infect oysters during their first year and cause heavy mortality at salinities >15 ppt, which are typical of Wreck Shoal, Brown Shoal, and Thomas Rock particularly in drought or low flow years (Fig. 2). Disease-related mortality increases thereafter with the majority of disease related deaths occurring during the first 2–3 y of life (Andrews 1996, Ford & Tripp 1996). The downward trend observed in the modern age at length relationship (Fig. 4B) between 1–1.6 y is probably related to the seasonal onset of Dermo with increasing temperatures (Burreson & Calvo 1996). Survival with infection is possible with potential side effects including reduced biomass or condition index and fecundity (Dermo; Paynter & Burreson 1991, MSX; Barber et al. 1988), and growth rates (Dermo; Menzel & Hopkins 1955, MSX; Matthiessen et al. 1990).

The mesohaline regions of the James River are still harvested as part of Virginia's oyster fishery. Legal market size (76 mm shell length) corresponds to oysters 2–3 y of age. Oysters that do manage to survive the effects of Dermo and MSX and reach larger sizes are also prime targets for the fishery. Consequently, 2–3-y-old oysters are under-represented in the modern populations (Fig. 3C to E) relative to the historic population demographic (Fig. 3A to B).

Water quality in the Chesapeake Bay has changed dramatically since the early 1600s. Descriptions of modern Chesapeake sedimentation rates are an order of magnitude higher than those observed in 1600 (Cooper & Brush 1993, Colman & Bratton 2003). Total organic carbon (TOC) levels from modern sediment cores are 2–5 times higher than TOC levels in 1600 (Cooper & Brush 1993, Cornwell et al. 1996, Zimmerman & Canuel 2002). The flux of biogenic silica to the benthos from diatoms, an index of diatom productivity, has also increased 4–5 times from the years 1600 to 2000 (Colman & Bratton 2003). Benthic foraminiferan species were dominant in 1600 but pelagic species (Cooper & Brush 1993) and relatively few benthic species tolerant of anaerobic conditions (Karlsen et al. 2000) dominate modern waters. Modern Chesapeake diatom communities favor species that grow under high nutrient conditions, that is eutrophication (Cooper & Brush 1993) instead of the original benthic species that thrived in clear waters. Zimmerman and Canuel (2002) describe an increase in dinoflagellates and cyanobacteria relative to benthic diatoms in Chesapeake Bay during the 20th century based on analysis of lipid biomarkers from sediment cores. Kennedy (1996) relates the shift from benthic to pelagic pathways to the coupled decline of the Chesapeake oyster resource with system-wide habitat degradation including increased sedimentation and runoff from shoreline development and destruction of natural reefs caused by harvest (Marshall 1954, Woods et al. 2005).

Observed changes in oyster demographics and growth rates across four centuries reflect changes in the environment as well as changes in oyster biology caused by chronic pressure from

two oyster diseases. Changes in these basic population parameters impact population biology as well as ecological function. Older (larger) oysters have a disproportionate effect on filtration rates, fecundity, and the creation of shell surface area (habitat) in that these three biological metrics increase nonlinearly with oyster shell length. In terms of the potential lifespan of the oyster (10–15 y, Powell & Cummins 1985), only the first third of the lifespan is currently represented in modern James River populations. Historic collections made by hand included a more complete demographic. It is likely that the upper end of the historic demographic was not vulnerable to collection by hand, and is underrepresented or not represented in James Fort well collections, because of the natural three-dimensional reef matrix in which multiple successive cohorts attached to previous generations (Hargis & Haven 1999, Powell & Klinck 2007, Mann & Powell 2007) that would have been present in the years 1606 to 1612. Environmental and epizootic stresses must be addressed to achieve any level of modern oyster

resource restoration to former levels of ecological and structural function.

ACKNOWLEDGMENTS

Dr. William Kelso, Beverly Straube, Daniel Schmidt, Caroline Taylor, and the staff of the Association for Preservation of Virginia Antiquities Jamestown Rediscovery Project provided access to the James Fort well oyster shells, laboratory space to measure them, and an invaluable archaeological perspective. Their assistance and enthusiasm are gratefully acknowledged. Dr. James A. Wesson, Adam Crockett, Vernon Rowe and the crew of the R/V *J.B. Baylor* have provided support for oyster surveys in Virginia waters since 1993. Thanks are extended to Bob & Joan Gonsoulin and Daniel & Jackie Billingsley for allowing us to use the Middle Ground lighthouse as a monitoring platform. This is contribution number 2969 from the Virginia Institute of Marine Science.

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