

Reconstructing early 17th century estuarine drought conditions from Jamestown oysters

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Oysters (*Crassostrea virginica*) were a central component of the Chesapeake Bay ecosystem in 1607 when European settlers established Jamestown, VA, the first permanent English settlement in North America. These estuarine bivalves were an important food resource during the early years of the James Fort (Jamestown) settlement while the colonists were struggling to survive in the face of inadequate supplies and a severe regional drought. Although oyster shells were discarded as trash after the oysters were eaten, the environmental and ecological data recorded in the bivalve geochemistry during shell deposition remain intact over centuries, thereby providing a unique window into conditions during the earliest Jamestown years. We compare oxygen isotope data from these 17th century oyster shells with modern shells to quantify and contrast estuarine salinity, season of oyster collection, and shell provenance during Jamestown colonization (1609–1616) and the 21st century. Data show that oysters were collected during an extended drought between fall 1611 and summer 1612. The drought shifted the 14 psu isohaline above Jamestown Island, facilitating individual oyster growth and extension of oyster habitat upriver toward the colony, thereby enhancing local oyster food resources. Data from distinct well layers suggest that the colonists also obtained oysters from reefs near Chesapeake Bay to augment oyster resources near Jamestown Island. The oyster shell season of harvest reconstructions suggest that these data come from either a 1611 well with a very short useful period or an undocumented older well abandoned by late 1611.

Chesapeake Bay | *Crassostrea virginica* | environmental reconstruction | oxygen isotope | scleroarchaeology

During the latter phases of sea level rise in the early Holocene, the Susquehanna River valley was inundated by the Atlantic Ocean, forming the modern Chesapeake Bay (1, 2). As sea level rose, eastern oysters (*Crassostrea virginica*) invaded the Bay, forming large populations and biogenic structures that expanded up the southern tributaries (1). By the early 17th century, self-perpetuating oyster populations dominated the system ecologically and spatially (1). Oysters provided habitat for numerous other species (3–5), created reef structures that delineated channels and funneled tidal flow (1, 6), enhanced bank stability between the estuary and tidal marshes (7), and provided a food resource for Native Americans (8). Dense oyster populations also provided ecological services that were central to estuarine trophic structure (9–11).

As the first settlers sailed up the James River in May 1607 and began construction of the James Fort on Jamestown Island (Fig. 1), they were unaware that the survival of the first permanent English settlement in North America would be intimately linked to local oyster populations. Although Jamestown was well established by the 1620s as the seat of colonial government (12, 13), shortages of food (14) and fresh drinking water (14, 15), combined with poor leadership (14, 15), nearly destroyed the colony during its first decade. The colonists had no way of knowing that their arrival in Virginia coincided with the beginning of a severe regional drought that included the driest 7 y (1606–1612) in nearly 8 centuries (16). The drought caused crop failures for the native Algonquin people (8, 14), reducing the likelihood that the colonists could successfully barter for large quantities of food. In May 1609, John Smith sent men downriver to live “on the oyster banks” for 9 wk to reduce pressure on meager food resources at the Fort (14, 17). During and immediately

after the winter of 1609–1610 (“The Starving Time”) (14), the settlers relied on oysters for food as they recovered from a winter in which ~44% of the colony died from causes including food and fresh water shortages (15).

Initially, a fresh water source was absent from Jamestown, and the colonists drank brackish James River water (14). The lack of fresh water likely contributed to the high mortality rates at Jamestown from 1607 to 1609 (15). Three Jamestown wells were documented from 1609 to 1624, although more may have been dug. In 1609 John Smith recorded the first well (14), and in May 1611 Governor Thomas Dale ordered construction of another well (14). The next well was documented in 1617 when Governor Samuel Argall either renovated the existing well or dug a new well to establish a reliable supply of fresh water (13).

Abandoned James Fort wells were filled with the colony’s trash including oyster shells (18). The infill is relevant archaeologically and the artifacts within a well provide insight into the time period and time course of well fill. Thus, archaeologists have concluded that a well [Association for the Preservation of Virginia Antiquities (APVA) Structure ID 170] discovered in 2003 just outside the James Fort containing artifacts dating to 1619–1625 is likely the Argall well of 1617 (13, 18).

During spring 2006, archaeologists discovered another well (APVA Structure ID 177; Fig. 2) within the James Fort (19) which is not clearly discernible as either the original Smith well or the Dale well on the basis of descriptive examination alone. Although this well cannot be from before 1609, foundations found directly over it date to 1617 (19), indicating that it was filled and capped by this date. Thus the period of use is limited to 1609–1616. Large numbers of oyster shells were part of the backfill in this well and form the foundation of this study.

The growth, life cycle, and ecology of *C. virginica* have been studied extensively from mid-Atlantic estuaries (20, 21). Within the Chesapeake Bay system, oyster shell growth occurs between ~8 and 25 °C (22). Each oyster shell contains a geochemical (¹⁸O/¹⁶O) record of growth, season of collection, estuarine temperatures and salinities (23, 24) and information that can identify locations of source oyster reefs. The James River and watershed have changed dramatically between 1607 and the present in terms of terrestrial vegetation (25), land use (25, 26), sedimentation rates (27, 28), nutrient sources (29, 30), and trophic structure (1, 9, 27, 30, 31). Because the James Fort well excavated in 2006 was abandoned and filled within a short time window, geochemical analyses of the oysters in this well provide an unparalleled opportunity to document estuarine environmental conditions during the earliest period of colonization. Thus, the Jamestown oysters provide a valuable

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Table 1. Morphological and geochemical description of modern Wreck Shoal (WS) and historic Jamestown Structure 177 (JT) oyster shells

Source	Shell ID	SL	SW	SL/SW ratio	Age (yr)	Avg $\delta^{18}\text{O}$	SD	$\delta^{18}\text{O}$ min	$\delta^{18}\text{O}$ max
WS	2	110	86	1.28	4.33	-4.74	1.12	-5.63	-2.84
	8	111	75	1.48	4.33	-4.26	1.37	-5.59	-2.64
	9	103	62	1.66	3.33	-4.8	0.9	-5.58	-2.73
	16	113	80	1.41	4.33	-4.55	1.29	-5.64	-2.58
JT	Z 1.2	148	94	1.57	3	-3.5	1.09	-4.4	-1.35
	Z 2.1	129	74	1.72	3.5	-3.62	1.58	-4.73	-0.97
	P 5.4	119	90	1.32	3.83	-3.38	1.46	-4.64	-1.18
	P 14.1	101	68	1.49	2.83	-3.5	1.19	-4.43	-1.16
	U 9.2	121	86	1.41	7.75	-3.52	1.1	-4.52	-1.42
	U 13.5	118	76	1.55	8.75	-3.4	0.8	-4.42	-1.97

Oxygen isotope data (Avg, SD, min, max) are presented graphically in Fig. S4. SL, shell length, maximum dimension from the hinge to the growth edge, mm; SW, shell width, maximum dimension perpendicular to shell length, mm; Age, age estimate based on oxygen isotope data corrected for collection month in years per Harding et al. (41); Avg, average; Max, maxima; Min, minima.

a pump was placed on the large wooden wellhead frame. It is possible that the accompanying volume of sediment might have ruined the well in a very short time.

The possibility also exists that Structure 177 is an earlier well dating to 1609 or 1610 and not the Dale well. If this well was dug in 1609 or 1610, it would have been used for at least a year before abandonment, infill, and the deposition of Z layer. The presence of a ceremonial halberd from Lord De La Warre's guard in AB layer (19) is noteworthy in that the halberd was not in Virginia before June 1610 and would not have been discarded until after De La Warre's departure in April 1611 (14). Other artifacts indicate that Structure 177 was in use when the halberd was discarded (19). An older well, in use during May 1611, is referred to by Dale as "...a new well for the amending of the most unwholesome waters which the old afforded..." (14, p. 523). The temporal sequence of fill for Structure 177 with late summer botanical material in AA and AB layers (19) combined with the oyster collections from Z (early winter 1611–1612), U and P layers (spring/early summer 1612) has parallels to the gradual conversion of an abandoned well to a trash pit beginning in mid-summer 1611. The season of harvest information from these shells combined with their stratigraphic sequence in the well describes either a 1611 well with a very short useful period or an undocumented older well abandoned in late 1611.

Historical Oyster Paleoenvironmental Implications. The complete $\delta^{18}\text{O}$ profiles obtained from Z and P layer oysters (Fig. 4 A–D) are similar to each other in terms of general seasonal trends and range of observed values (-0.3 to -5.7 ‰), suggesting that these oysters were collected from reef(s) with similar seasonal T and S conditions. This conclusion is also supported by a comparison of average minimum and maximum shell $\delta^{18}\text{O}$ values between these shells, which indicates that the P and Z layer $\delta^{18}\text{O}$ data are indistinguishable (Table 1 and Fig. S4).

Unlike the Z and P layer shells, the $\delta^{18}\text{O}$ profiles from U layer oysters (Fig. 5 A and B) display seasonal cycles that reflect lower annual growth rates and, in general, record a narrower range of $\delta^{18}\text{O}$ values. Although summer (minimum) U layer $\delta^{18}\text{O}$ values are similar to Z and P layer $\delta^{18}\text{O}$ minima (Figs. 4 A–D and 5 C and D), U layer winter maxima values are lower than either Z or P layer shells. If we assume that U layer oysters stopped calcifying below 8°C and above 25°C (similar to modern WS oysters), then the geochemical differences indicate that U layer oysters were collected from a reef that was exposed to less saline winter conditions than oysters from the Z and P layers. Thus, we will discuss the U layer shells separately.

Z and P layer oysters display an annual seasonal $\delta^{18}\text{O}$ cycle that is similar in duration to modern WS oysters (Fig. 4). However, the average "historical" summer (-4.55 ± 0.16 ‰) and winter (-1.16 ± 0.16 ‰) values are 1.06 ‰ and 1.54 ‰ more positive, respectively, than corresponding average modern WS summer (-5.61 ± 0.03 ‰) and winter (-2.70 ± 0.16 ‰) values (Table 1 and Fig. S4). If we

assume that growth was constrained by temperature limits of 25°C and 8°C , then we can compute summer and winter salinities by first computing $\delta^{18}\text{O}_{\text{water}}$ from Eq. 3 and converting these values to salinity with Eq. 1. Here, we are assuming the $\delta^{18}\text{O}_{\text{water}}$ vs. S relationship of the James River during the early 1600s was similar to that of modern times and that the most likely source(s) of the Z and P layer oysters were reefs near JI above MP (Fig. 1). The resulting average summer and winter salinities are 18.4 psu ($\delta^{18}\text{O}_{\text{water}} = -2.48$ ‰) and 16 psu ($\delta^{18}\text{O}_{\text{water}} = -3.08$ ‰), respectively. Whereas the calculated summer S is similar to that for the modern WS oysters during the drier summer season, the historic Jamestown winter S is considerably higher than modern. These data confirm a significant reduction in winter precipitation over the James River between 1609 and 1612 compared with precipitation between 2002 and 2006, in agreement with documentation of drought conditions at that time (16).

Drought of 1606–1612 and Implications for Historical Oyster Ecology.

Severe regional drought between 1606 and 1612 has been described independently using tree rings (16), benthic foraminifera (39, 40), and pollen data (25). The suggestion that regional salinities in the Chesapeake Bay increased by 10 – 15 psu during 1606–1612 relative to modern salinities (40) is in agreement with our winter salinity estimates from Z and P layer oysters. Thus, James River salinities between JI and MP (Fig. 1) would have been mesohaline (10 – 23 psu) year round during the 1606–1612 drought.

Maps by Tyndall (1608; 14) and Vingaboons (1617; 13) record oysters in the James River as far upriver as the mouth of the

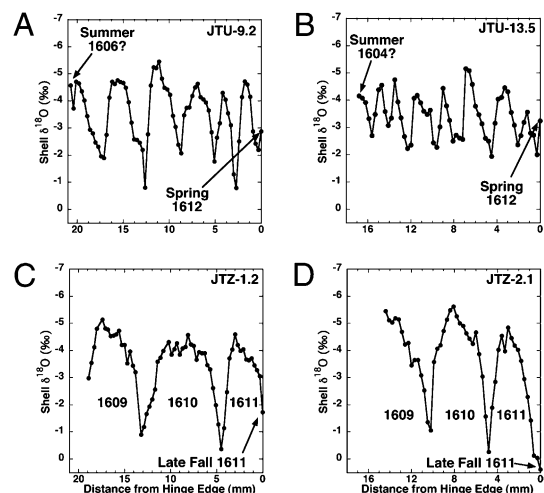


Fig. 5. Measured $\delta^{18}\text{O}$ data from historic oyster shells from high-salinity (A and B) and medium-salinity (C and D) environments.

Chickahominy River above JI (Fig. 1). It is likely that the severity and duration of the 1606–1612 drought would have facilitated the upriver expansion of oyster habitat from MP toward JI. The drought would have shifted the James River salinity gradient upriver through a combination of increased tidal incursion and a 40–50% reduction in freshwater discharge (40). Beginning in 1606, drought induced salinities of 14 psu (38) between JI and MP would have encouraged oyster recruitment. By 1608, reefs could have formed near Jamestown containing oysters suitably sized for food (~2-yr-old oysters, *SI Text*) (41) within easy access for the colonists.

Environmental and Historical Implications of U Layer Oyster Geochemistry.

Based on the stratigraphic relationship of the U layer between Z and P layers and our reconstruction of the collection timing of the Z and P layer oysters, we infer that U layer shells were harvested during spring/early summer 1612, given the range of hinge edge values (Fig. 5*A* and *B* and *Table S1*). Age estimates using winter $\delta^{18}\text{O}$ maxima indicate that U layer oysters were older at collection than the other oysters examined (Table 1) and appear to have settled before the drought began (1604 or 1605; Fig. 5).

Of particular interest is the uniqueness of the U layer $\delta^{18}\text{O}$ records relative to WS, Z and P layer oysters. First, the U layer $\delta^{18}\text{O}$ records contain 5–7 yr of seasonal signal in contrast to the 3–4 yr of growth documented in the other shells (Figs. 4 and 5). Second, although the average $\delta^{18}\text{O}$ minima (summer, $-4.47 \pm 0.07\text{‰}$) in oysters U 9.2 and 13.5 are indistinguishable from the Z and P layer shells, the average $\delta^{18}\text{O}$ maxima (winter, $-1.70 \pm 0.39\text{‰}$) are more negative than Z and P layer maxima ($>0.5\text{‰}$; Table 1 and Fig. S4). This suggests fresher winter conditions or minimum temperatures that did not drop below 8 °C (Table 1 and Figs. 4 and 5). We prefer the former explanation, as it is unlikely that winter/summer extreme temperatures varied much across the James River oyster habitat. Oxygen isotope data from Z and P layer shells are in agreement with modern water temperature and oxygen isotope data which show that James River temperatures are below 8 °C for at least a short period each year (Fig. 3 and Fig. S5). An intertidal harvest site in a small watershed close to the James River confluence with the Chesapeake Bay could explain the U layer $\delta^{18}\text{O}$ signal.

Shell U9.2 (Fig. 5*A*) displays $\delta^{18}\text{O}$ values and growth cycles of the same timing and magnitude (0 to -5‰) predicted by the annual salinity cycle at OPC (Figs. 1 and S5C), although the $\delta^{18}\text{O}$ pattern recorded in shell U13.5 displays a smaller range than that in U9.2 (comparing Fig. 5*A* vs. *B*). The maxima of -0.5‰ displayed by shell U9.2 in the winters of 1609–1610 and 1607–1608 are absent in U13.5. If U13.5 grew closer to the air–water interface on the source intertidal oyster reef than U9.2, this shell would have been exposed at low tide more often and for longer periods than U9.2. Exposure to air and relatively shallow water would be commensurate with longer and more intense exposure to temperatures above or below the 8–25 °C window required for calcification, thereby resulting in a truncated or compressed growth trajectory of U13.5 relative to U9.2 and the Z and P layer shells. Furthermore, shallow exposure would have exposed the oysters to the less saline near surface estuarine layer, thereby explaining the reduced U layer winter $\delta^{18}\text{O}$ maxima values.

Given the temporal relationship of the Z, U and P layers combined with the unique U layer stable isotope records, we hypothesize that the U layer oysters were transported to Jamestown from a downriver tributary source closer to the James River confluence with the Chesapeake Bay. By 1612, the colonists had established settlements between the Hampton River and Mill Creek (Ft. Algernonne; Fig. 1) and on the Nansemond River (17) (Fig. 1) and had contact with Native American settlements in the Elizabeth River drainage (Fig. 1). All four of these tributaries historically supported oysters (14, 42). Upon their arrival in the Chesapeake Bay, ships from England typically stopped at Ft. Algernonne (Fig. 1) before proceeding upriver to Jamestown. Both Nansemond and Hampton River oysters would have been accessible to supply ships moving upriver from Ft. Algernonne. The region around Ft. Algernonne was also identified by colonists as a reliable source of oysters, crabs, and fish because of its proximity to the Bay and the Atlantic Ocean (14). The colony had a shallow draft “barge” (8) that could have been used to harvest and

transport shellfish upriver independently of larger supply ships. By spring 1612, the number of colonists at Jamestown had increased, whereas their mortality rate had decreased (15). This net population increase combined with years of harvest pressure was probably a strain on the oysters near JI and transport of seafood upriver by ships was likely necessary to keep Jamestown adequately supplied.

Conclusion

The James River was a different habitat in the early 17th century than it is today. Oyster shells from James Fort Structure 177 document estuarine conditions during the 1606–1612 drought, thereby providing an estuarine analog to the terrestrial bald cypress chronologies (16) as well as a unique view of the James River and Jamestown during the earliest years when the colony was fighting to survive. Although the drought presented numerous challenges for the colonists, conditions in the estuary may have facilitated oyster growth and extension of habitat upriver as more saline conditions migrated above JI. Despite reefs near JI, the colonists appear to have augmented local resources with oysters from reefs near the Chesapeake Bay. The oyster shell season of harvest information combined with their stratigraphic relationships in the well describe either a 1611 well with a very short useful period or an undocumented older well abandoned by late 1611. Because oysters are finely tuned stationary barometers in historic and modern estuarine environments, they are a critical source of paleoecological, paleoenvironmental, and archaeological information for studies of early colonization of the New World.

Materials and Methods

Oyster Shell Sources. In spring 2006, APVA archaeologists excavating a Jamestown well (APVA Structure ID 177, Fig. 1) categorized material that was removed into 29 layers (Fig. 2) on the basis of its apparent coherence within geologic features and archaeological context (19). Layers AC (deepest, bottom of well) through D (shallow) correspond to a coherent time period within the colony between 1609 and 1616 (19). There was no mixing of artifacts from within the well with those from later time periods beginning with layer N (19) (Fig. 2). Intact left oyster shell valves were selected from three well layers: P ($n = 6$, relatively shallow), U ($n = 6$, intermediate), and Z ($n = 4$, deep) for stable isotope analyses. These layers were selected because they span the available depth profile and each had a relatively large number of intact left valves (483, 726, and 166 intact valves, respectively for the P, U, and Z layers).

For comparative purposes, live oysters were collected from WS ($n = 4$) during November 2006 and killed to obtain modern left oyster valves with a known collection date. Only left valves with a straight resilium were used in this study (41). Oyster shells were embedded and sectioned along a straight axis extending from the hinge to the growth edge through the resilium parallel to the axis of maximum growth (23, 44).

Geochemical Sample Collection and Analyses. Oyster shell sections were mounted on a computer-aided triaxial sampler (45). For two shells from each layer, samples were collected every 0.3 mm along a 0.8-mm-wide path drilled near the resilium from the outer (oldest) to the inner (youngest) layer. Transects were drilled perpendicular to growth bands using a 0.5-mm carbide dental burr. In the remaining shells from each layer, samples were collected from the most recent 10 mm of the internal shell margin to encompass the last ~6 months of life. Powdered shell calcite was collected and roasted in vacuo for 30 min at 375 °C before analysis on a Fisons Optima isotope ratio mass spectrometer using an Isocarb common acid bath device. Acid reaction temperature was 90 °C. Water $\delta^{18}\text{O}$ was determined via CO_2 equilibration using an automated equilibrator attached to a Finnigan MAT 251 isotope ratio mass spectrometer.

All oxygen isotope data are presented relative to the Vienna Pee Dee Belemnite (V-PDB) standard, whereas water oxygen isotope data are presented relative to Vienna Standard Mean Ocean Water (V-SMOW) standard. Data are presented in standard per mil (‰) notation where:

$$\delta^{18}\text{O} = \left[\left(\frac{{}^{18}\text{O}}{{}^{16}\text{O}}_{\text{sample}} / \frac{{}^{18}\text{O}}{{}^{16}\text{O}}_{\text{std}} \right) - 1 \right] \times 1,000$$

Analytical precision ($\pm 1 \sigma$) of the carbonate $\delta^{18}\text{O}$ data was $\pm 0.06\text{‰}$ based on repeat analyses of an in-house calcite standard. The precision of water replicates was $\pm 0.03\text{‰}$ ($\pm 1 \sigma$).

Data Analyses: Relationship Between Salinity and $\delta^{18}\text{O}_{\text{water}}$. Water samples from WS and MG in the James River (Fig. 1) were analyzed for salinity and stored in sealed vials for $\delta^{18}\text{O}$ analyses (*SI Text*). Relationships between sa-

linity and $\delta^{18}\text{O}_{\text{water}}$ ($=\delta^{18}\text{O}_w$) were calculated for WS and MG waters (Fig. S3) using linear regression analyses, yielding:

$$\delta^{18}\text{O}_w (\text{WS}) = 0.25 * S - 7.08 \text{ (Fig. S3, } R^2 = 0.80, n = 11) \quad [1]$$

$$\delta^{18}\text{O}_w (\text{MG}) = 0.21 * S - 6.99 \text{ (Fig. S3, } R^2 = 0.99, n = 3) \quad [2]$$

We compute a predicted $\delta^{18}\text{O}_{\text{calcite}}$ ($=\delta^{18}\text{O}_c$) time series for oysters growing between 2002–2006 by combining water temperatures (T) from WS (SI Text) and $\delta^{18}\text{O}_w$ values computed from Eq. 1 by inverting the T vs. $\delta^{18}\text{O}_{\text{calcite}}$ relationship of Epstein et al. (46).

$$T = 16.5 - 4.30 (\delta^{18}\text{O}_c - \delta^{18}\text{O}_w) + 0.14 * (\delta^{18}\text{O}_c - \delta^{18}\text{O}_w)^2 \quad [3]$$

to yield

$$\delta^{18}\text{O}_c = \delta^{18}\text{O}_w - 0.20 + (4.30 - (18.49 - 0.56 * (16.5 - T)^{0.5}) / (0.28)) \quad [4]$$

Here, 0.20‰ is subtracted from $\delta^{18}\text{O}_w$ to correct for the V-PDB and V-SMOW differences in this relationship (47). Similar predictions are made for Old Point Comfort (Fig. 1) using Eq. 2.

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- Hargis WJ, Jr. (1999) *Oyster Reef Habitat Restoration: A Synopsis of Approaches*, eds Luckenbach MW, Mann R, Wesson JA (Virginia Institute of Marine Science, Gloucester Point, VA), pp 5–24.
- Hobbs C (2004) Geological history of Chesapeake Bay, USA. *Quat Sci Rev* 23:641–661.
- Wells H (1961) The fauna of oyster beds, with special reference to the salinity factor. *Ecol Monogr* 31:239–266.
- Coen L, Luckenbach M, Breitburg D (1999) *Fish Habitat: Essential Fish Habitat and Rehabilitation*, ed Benaka LR. Am Fish Soc Symp 22 (Bethesda, MD), pp 438–454.
- Harding JM, Mann R (1999) Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. *Bull Mar Sci* 65:289–300.
- DeAlteris J (1988) The geomorphic development of Wreck Shoal, a subtidal oyster reef of the James River, Virginia. *Estuaries* 11:240–249.
- Bahr L, Lanier W (1981) *The Ecology of Intertidal Oyster Reefs of the South Atlantic Coast: A Community Profile*. US Fish and Wildlife Series (US FWS, Washington, DC). FWS/OBS-81/15.
- Rountree HC, Clark W, Mountford K (2007) *John Smith's Chesapeake Voyages: 1607–1609* (Univ of VA Press, Charlottesville), pp 12–15, 48, 66–67, 131.
- Newell RIE (1988) *Understanding the Estuary: Advances in Chesapeake Bay Research*, eds Lynch MP, Krome EC. (Chesapeake Research Consortium, Gloucester Point, VA), pp 536–546.
- Ulanowicz RE, Tuttle JH (1992) The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries* 15:298–306.
- Newell RIE, Fisher TR, Holyoke RR, Cornwell JC (2005) *The Comparative Roles of Suspension Feeders in Ecosystems*, eds Dame R, Olenin S. Vol 47, NATO Series: IV—Earth and Environmental Sciences (Springer, The Netherlands), pp 93–120.
- Hatch CE (1957) *The First Seventeen Years: Virginia, 1607–1624* (Univ of VA Press, Charlottesville), pp 4–34.
- Kelso W (2006) *Jamestown: The Buried Truth* (Univ of VA Press, Charlottesville), pp 11–27, 89–93, 115–124.
- Haile EW (1998) *Jamestown Narratives: Eyewitness Accounts of the Virginia Colony* (Roundhouse Publishers, Champlain, VA), pp 96–100, 118–120, 128–129, 319–343, 416–431, 497–519.
- Earle CV (1979) *The Chesapeake in the Seventeenth Century: Essays on Anglo-American society*, eds Tate T, Ammerman D (Univ of NC Press, Chapel Hill), pp 97–125.
- Stahle DW, Cleaveland MK, Blanton DB, Therrell MD, Gay DA (1998) The lost colony and Jamestown droughts. *Science* 280:564–567.
- Brown A (1898) *The First Republic in America, An Account of the Origin of this Nation Written from Records then (1624) Concealed by the Council rather than from the Histories then Licensed by the Crown* (Houghton Mifflin, New York), pp 68–125.
- Kelso W, Straube B (2004) *Jamestown Rediscovery 1994–2004* (Association for the Preservation of Virginia Antiquities, Richmond, VA), pp 131–135.
- Kelso W, Straube B (eds) (2008) *2000–2006 Interim Report on the APVA excavations at Jamestown Virginia*, (Association for the Preservation of Virginia's Antiquities, Richmond, VA), pp 55–69.
- Brooks WK (1891) *The Oyster* (Johns Hopkins Univ Press, Baltimore), p 230.
- Galtsoff P (1964) The American Oyster *Crassostrea virginica* Gmelin. *US Fish Wildlife Service Fish Bull* 64, pp 397–456.
- Mann R, Evans D (2004) Site selection for oyster habitat rehabilitation in the Virginia portion of the Chesapeake Bay. *J Shellfish Res* 23:41–49.
- Kirby MX, Soniat T, Spero HJ (1998) Stable isotope sclerochronology of Pleistocene and recent oyster shells (*Crassostrea virginica*). *Palaios* 13:560–569.
- Surge D, Lohmann K, Dettman D (2001) Controls on isotopic chemistry of the American oyster, *Crassostrea virginica*: Implications for growth patterns. *Palaogeogr Palaeoclimatol Palaeoecol* 172:283–296.
- Brush G (2001) Natural and anthropogenic changes in Chesapeake Bay during the last 1000 years. *Hum Ecol Risk Assess* 7:1283–1296.
- Brush G (1986) Geology and Paleocology of Chesapeake Bay: A long-term monitoring tool for management. *J Wash Acad Sci* 76:146–160.
- Cooper S, Brush G (1993) A 2,500 year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries* 16(3B):617–626.
- Colman S, Bratton J (2003) Anthropogenically induced changes in sediment and biogenic silica fluxes in Chesapeake Bay. *Geology* 31:71–74.
- Cornwell J, Conley D, Owens M, Stevenson J (1996) A sediment chronology of the eutrophication of the Chesapeake Bay. *Estuaries* 19:488–499.
- Zimmerman A, Canuel E (2002) Sediment geochemical records of eutrophication in the mesohaline Chesapeake Bay. *Limnol Oceanogr* 47:1084–1093.
- Kennedy V (1996) The ecological role of the eastern oyster, *Crassostrea virginica*, with remarks on disease. *J Shellfish Res* 15:177–183.
- Nichols M (1972) *Sediments of the James River Estuary, Virginia*. The Geological Society of America. The GSA Memoir 133 (Geological Society of America, New York, NY), pp 169–212.
- Brooks T, Fang C (1983) James River slack water data report: Temperature, salinity, and dissolved oxygen 1971–1980. VIMS Data Report No. 12 (Virginia Institute of Marine Science, Gloucester Point, VA).
- Mann R, Southworth MJ, Harding JM, Wesson JA (2009) Population studies of the native oyster, *Crassostrea virginica* (Gmelin, 1791), in the James River, Virginia, USA. *J Shellfish Res* 28:193–220.
- Haven DS, Whitcomb JP (1983) The origin and extent of oyster reefs in the James River, Virginia. *J Shellfish Res* 3:141–151.
- Mann R, Evans D (1998) Estimation of oyster, *Crassostrea virginica*, standing stock, larval production and advective loss in relation to observed recruitment in the James River, Virginia. *J Shellfish Res* 17:239–254.
- Gunter G (1950) Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. *Publ Inst Mar Sci Univ Texas* 1:7–51.
- Ellison RL, Nichols M (1976) Modern and holocene foraminifera in the Chesapeake Bay region. Maritime Sediments Special Publication 1. 1st International Symposia on Benthic Foraminifera of Continental Margins, (Dalhousie University, Halifax, Nova Scotia), pp 131–151.
- Karlsen A, et al. (2000) Historical trends in Chesapeake Bay dissolved oxygen based on benthic foraminifera from sediment cores. *Estuaries* 23:488–508.
- Cronin T, et al. (2000) Climatic variability in the eastern United States over the past millennium from Chesapeake Bay sediments. *Geology* 28:3–6.
- Harding JM, Mann R, Southworth MJ (2008) Shell length-at-age relationships in James River oysters (*Crassostrea virginica*) collected four centuries apart. *J Shellfish Res* 27:1109–1115.
- Baylor JB (1896) *Method of Defining and Locating Natural Oyster Beds, Rocks and Shoals. Oyster Records (pamphlets, one for each Tidewater, Virginia county)* (Board of Fisheries of VA Richmond, VA).
- Surge D, Lohmann K, Goodfriend G (2003) Reconstructing estuarine conditions: Oyster shells as recorders of environmental change, Southwest Florida. *Estuar Coast Shelf Sci* 57:737–756.
- Harding JM, Mann R (2006) Age and growth of wild suminoe (*Crassostrea ariakensis*, Fugita 1913) and Pacific (*C. gigas*, Thunberg 1793) oysters from Laizhou Bay, China. *J Shellfish Res* 25:73–82.
- Quinn T, Taylor F, Crowley T, Link S (1996) Evaluation of sampling resolution in coral stable isotope records: A case study using records from New Caledonia and Tarawa. *Paleoceanography* 11:529–542.
- Epstein S, Buchsbaum R, Lowenstam H, Urey H (1953) Revised carbonate water isotopic temperature scale. *Geol Soc Am Bull* 2:417–425.
- Bemis BE, Spero HJ, Bijma J, Lea DW (1998) Reevaluation of the oxygen isotope composition of planktonic foraminifera: Experimental results and revised paleotemperature equations. *Paleoceanography* 13:150–160.

Supporting Information

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SI Text

Environmental Data for Oxygen Isotope Calibrations. The oyster population at Wreck Shoal in the James River, VA (Fig. 1 and Fig. S1, 37.06 N, -76.57 W), ~34 km southeast of Jamestown, was sampled as part of ongoing Virginia Institute of Marine Science (VIMS) monitoring studies at least every 3 months from October to May and weekly from May to October during 2002–2006. Water temperature (T, °C) and salinity (S, psu) were recorded 0.5 m from the bottom during each sampling trip. VIMS maintains a hydrographic monitoring station that records bottom T and S with 15-min resolution at Gloucester Point on the York River (37.2475 N, -76.4994 W). York and James River T are temporally equivalent (1), so York River T data were used as a surrogate for Wreck Shoal T when the latter were unavailable. Bottom T and S data from 2002 to 2006 at Old Point Comfort (Fig. 1, 36.00 N, -76.31 W; http://www.chesapeakebay.net/data_waterquality.aspx) are used to describe annual T and S conditions at a higher-salinity location. Water samples for oxygen isotope ($\delta^{18}\text{O}_{\text{water}}$) analyses collected from Wreck Shoal (August 2006 to September 2007) and Middle Ground (December 2006 to August 2007) (Fig. 1) provide a dataset from which modern James River $\delta^{18}\text{O}_{\text{calcite}}$ values are predicted.

Oyster Measurements and Morphology. Oysters do not grow symmetrically and are plastic with regard to morphological form. Shell length (SL) and shell width (SW) were measured (mm) for each left valve. SL, the longest dimension from the hinge to the shell growth margin is correctly termed shell height but is commonly described as SL in most literature. We adopt the common convention and refer to SL in the subsequent text. SW is the maximum dimension perpendicular to SL. Ratios of SL to SW can be used to characterize oyster morphological forms (2). Harding et al. (3) considered only WS and Jamestown oysters (from the same well examined by this study) with SL to SW ratios less than 1.9 to ensure that only similar growth forms were being com-

pared. The SL to SW ratios of the WS shells examined here are also less than 1.9 (Table 1) and can be compared with these data (3). The SL to SW ratios for Z and P layer shells, like those of the modern WS shells, are less than 1.9 (Table 1).

Oyster Age-at-Length Determinations from Oxygen Isotope Data.

The isotope profiles in Figs. 4 and 5 record oyster growth from the outer (oldest) edge of the shell cross-section just above the resilium to the inner (most recent, 0 value) edge. For example, the first year of the life of WS 8 extends from ~21 through ~11.5 mm (Fig. 4F), with year 2 from ~11.5 to ~5.5 mm, year 3 from ~5.5 to ~2.5 mm, and year 4 from ~2.5–0 mm. Thus, WS 8 was in its fourth year of growth when it was collected in November 2006 (Table 1), and we assign it an age of 4 based on the number of oxygen maxima (winter values) observed in the isotope record. Enumeration of the observed oxygen maxima for WS 2, 9, and 16 yield age (yr) estimates of 4, 3, and 4, respectively (Table 1). Adjustment of the age estimates for collection date (November), assuming a birth date of July 1 (1, 3), adds 0.33 to each age. Oxygen isotope derived age-length relationships from these four WS oysters are in agreement with those previously described for WS oysters using cohort analyses (3) (Fig. S2).

As with the WS shells, enumeration of $\delta^{18}\text{O}$ maxima (winter values) in the Jamestown shells provides an estimate of age (yr) at the time of collection. Examination of the Z1.2 isotope profile shows the first year of growth from ~19–14 mm, year 2 from ~14 to ~4 mm, and the final year from ~4–0 mm (Fig. 4A–D). Age estimates (yr) for these shells are 2.5, 3, 3, and 2 for Z1.2, Z2.1, P14.1, and P5.4, respectively (Table 1). Age (yr) estimates for historic shells have also been adjusted for the collection season assuming a July 1 birth date (1, 3) (Table 1) by adding 0.5, 0.75, and 0.83 to Z, U, and P layer age estimates, respectively. The resulting isotopic age-at-length descriptions for Z and P oysters are in agreement with those previously described for historic oysters (3) (Fig. S2).

1. Mann R, Southworth MJ, Harding JM, Wesson JA (2009) Population studies of the native oyster, *Crassostrea virginica* (Gmelin, 1791), in the James River, Virginia, USA. *J Shellfish Res* 28:193–220.
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3. Harding JM, Mann R, Southworth MJ (2008) Shell length-at-age relationships in James River oysters (*Crassostrea virginica*) collected four centuries apart. *J Shellfish Res* 27: 1109–1115.

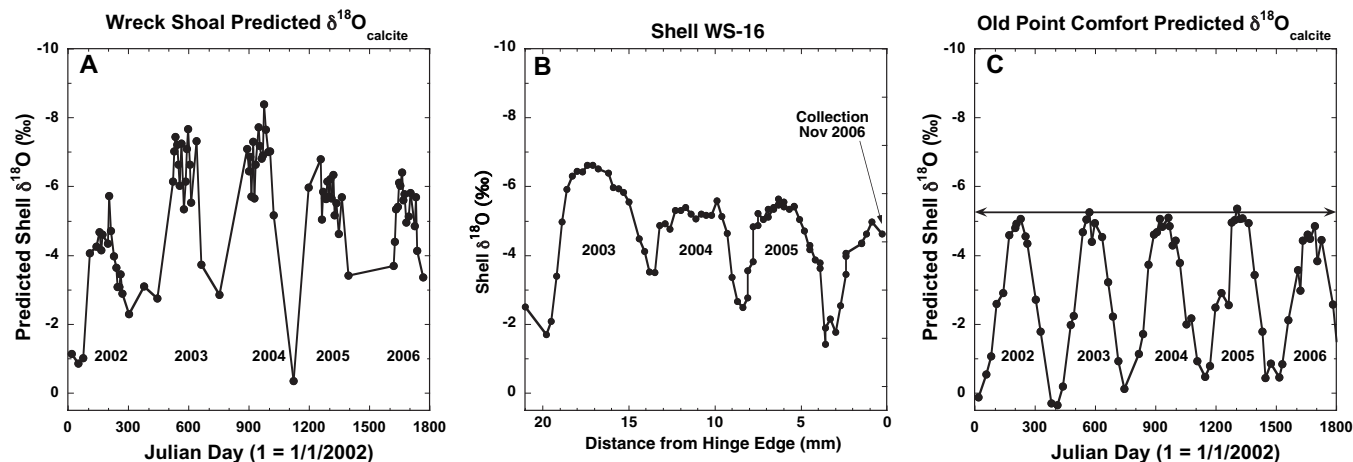


Fig. S5. Predicted $\delta^{18}\text{O}_{\text{calcite}}$ values for Wreck Shoal shells from 2002 through 2006 (A) with observed $\delta^{18}\text{O}$ values from modern shell WS16 (B) and predicted $\delta^{18}\text{O}_{\text{calcite}}$ values from the higher salinity Old Point Comfort region during 2002–2006 (C). Horizontal line with arrows (C) denotes the predicted summer minima at Old Point Comfort in contrast to the predicted minima at the lower salinity Wreck Shoal (A) during the same years.

Table S1. Final edge $\delta^{18}\text{O}$ values from Jamestown oyster shells sampled in this study

Shell ID	Final shell $\delta^{18}\text{O}$	Layer mean $\delta^{18}\text{O} \pm 1\sigma$
P12.2	−5.39	$−3.77 \pm 1.44$
P14.2	−3.43	
P14.3	−3.74	
P6.3	−1.17	
P14.1*	−4.46	
P5.4*	−4.40	$−3.96 \pm 1.20$
U12.2	−4.90	
U13.6	−5.65	
U8.2	−2.69	
U9.1	−4.37	
U9.2*	−2.88	$−0.77 \pm 0.94$
U13.5*	−3.24	
Z2.3	−1.32	
Z3.2	−0.42	
Z2.1*	0.39	
Z1.2*	−1.72	

Letters in shell identification code (Shell ID) correspond to well layer (P, U, or Z; Fig. 2) from which oysters were collected. Final edge $\delta^{18}\text{O}$ values from Z layer are significantly more positive than values from U and P layers (ANOVA, $F = 9.24$, $P = 0.003$).

*Specimens with full hinge isotope records presented in body of text.