Millennial-scale sustainability of the Chesapeake Bay Native American oyster fishery

Torben C. Rick[a,1], Leslie A. Reeder-Myers[a], Courtney A. Hofman[a,b], Denise Breitburg[c], Rowan Lockwood[d], Gregory Henkes[e], Lisa Kellogg[f], Darrin Lowery[g], Mark W. Luckenbach[f], Roger Mann[f], Matthew B. Ogburn[c], Melissa Southworth[f], John Wah[h], James Wesson[i], and Anson H. Hines[c]

[a]Program in Human Ecology and Archaeobiology, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013; [b]Department of Anthropology, University of Oklahoma, Norman, OK 73019; [c]Smithsonian Environmental Research Center, Edgewater, MD 21037; [d]Department of Geology, College of William and Mary, Williamsburg, VA 23187; [e]Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD 21218; [f]Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062; [g]Chesapeake Watershed Archaeological Resources, Easton, MD 21601; [h]Matapeake Soil, Shippensburg, PA 17257; and [i]Virginia Marine Resources Commission, Newport News, VA 23607

Edited by Patrick V. Kirch, University of California, Berkeley, CA, and approved April 21, 2016 (received for review January 1, 2016)

Estuaries around the world are in a state of decline following decades or more of overfishing, pollution, and climate change. Oysters (Ostreidae), ecosystem engineers in many estuaries, influence water quality, construct habitat, and provide food for humans and wildlife. In North America's Chesapeake Bay, once-thriving eastern oyster (*Crassostrea virginica*) populations have declined dramatically, making their restoration and conservation extremely challenging. Here we present data on oyster size and human harvest from Chesapeake Bay archaeological sites spanning ~3,500 y of Native American, colonial, and historical occupation. We compare oysters from archaeological sites with Pleistocene oyster reefs that existed before human harvest, modern oyster reefs, and other records of human oyster harvest from around the world. Native American fisheries were focused on nearshore oysters and were likely harvested at a rate that was sustainable over centuries to millennia, despite changing Holocene climatic conditions and sea-level rise. These data document resilience in oyster populations under long-term Native American harvest, sea-level rise, and climate change; provide context for managing modern oyster fisheries in the Chesapeake Bay and elsewhere around the world; and demonstrate an interdisciplinary approach that can be applied broadly to other fisheries.

historical baseline | archaeological shellfish | fossil shellfish | marine fisheries | environmental management

Home to rich and productive ecosystems, estuaries have long been attractive places for human settlement and subsistence. Following decades or more of overfishing, pollution, and other perturbations, estuaries and bays around the world are in a dramatic state of decline (1, 2). Oysters (Ostreidae) are ecosystem engineers in many estuaries, providing a variety of ecosystem services including water filtration and habitat construction for other organisms (3–6). Oysters have also long been an attractive food source for people, including those living near North America's Chesapeake Bay (7–10).

With a watershed spanning ~166,000 km^2, the Chesapeake Bay is the largest estuary in the continental United States and once supported a massive commercial oyster fishery (8). In the late 1800s, some 400–600,000 tons of oysters were harvested from the Chesapeake annually, which resulted in depletion and overfishing. Harvests decreased by as much as 50% by the early 1900s and 98% by the early 1990s (8, 11). This was part of a larger process termed "fishing down the coast," with historical overharvest of oysters occurring first in Massachusetts and New York estuaries and then southward to the Chesapeake Bay and the Gulf of Mexico (12). Several US estuaries, including the Chesapeake Bay, experienced declines in oysters as part of a broader pattern of historical reductions in a variety of estuarine organisms (6, 8).

Although the precise numbers are debated, oyster populations in Maryland's waters today are estimated to represent less than 1% of their historical abundance (13) and, although some Virginia oyster populations have shown signs of improvement (5, 14), they are not much more abundant. This precipitous decline makes it difficult to establish baselines, adding to the already difficult task of restoring a sustainable fishery in the face of ongoing harvest, eutrophication, sedimentation, and disease (15). In the 17th century, Captain John Smith and other early colonists reported on the bounty of the Chesapeake, including its massive, widespread oyster reefs (16). These early accounts are largely anecdotal, but some scholars have speculated that oysters were so plentiful during this time that they could filter a volume of water equal to that in the Chesapeake in just a few days (17, 18). Catch records provide empirical data on the oyster fishery but they begin in the 1870s, after the bay had already been the focus of intensive historical harvest (8). Given the current state of decline and the major changes forecast for Anthropocene climate and ecology (e.g., increased climatic warming and instability, acidification, and invasive species), a return to the abundance witnessed by John Smith is not feasible, leaving a gap between ideal restoration goals and reality (15).

A key element missing from discussions of past oyster abundance and population structure is a comprehensive understanding of the fishery before historical overfishing (5, 6, 8, 11). Native Americans have lived in the Chesapeake region since the late Pleistocene (>13,000 y ago), when it was part of the Susquehanna River valley, throughout the Holocene submergence of the valley

Significance

Oysters are important organisms in estuaries around the world, influencing water quality, constructing habitat, and providing food for humans and wildlife. Following over a century of overfishing, pollution, disease, and habitat degradation, oyster populations in the Chesapeake Bay and elsewhere have declined dramatically. Despite providing food for humans for millennia, we know little about Chesapeake Bay oyster populations prior to historical fishing in the late 1800s. Using fossil, archaeological, and modern biological data, we reconstruct changes in oyster size from the Pleistocene and prior to human harvest through prehistoric Native American occupation and modern times. These data demonstrate sustainability in the Native American oyster fishery, providing insight into the future management of oysters in the Chesapeake Bay and around the world.

Author contributions: T.C.R. and L.A.R.-M. designed research; T.C.R., L.A.R.-M., C.A.H., R.L., G.H., L.K., D.L., M.W.L., R.M., M.B.O., M.S., J. Wah, J. Wesson, and A.H.H. performed research; D.B., R.L., G.H., L.K., M.W.L., R.M., M.B.O., M.S., J. Wesson, and A.H.H. contributed data; T.C.R., L.A.R.-M., C.A.H., D.B., and R.L. analyzed data; and T.C.R., L.A.R.-M., C.A.H., D.B., and R.L. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. Email: rickt@si.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1600019113/-/DCSupplemental.

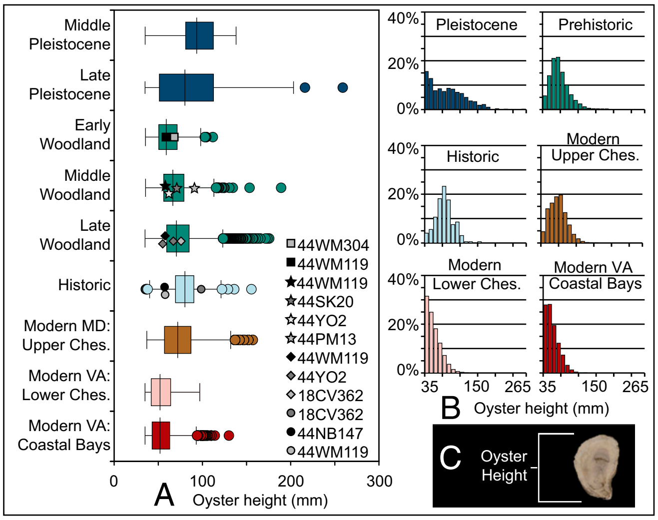

Fig. 1. Comparison of Chesapeake Bay oyster height measurements through time for fossil, archaeological, and modern assemblages. (*A*) The box-and-whisker plots used in this study display data according to the following guidelines: The tall central line represents the median of the data; the box represents data between the first and third quartiles; whiskers represent data within 1.5× the interquartile range of the median; and circles represent data within 3× the interquartile range of the median. Archaeological site trinomials are listed on the right (*SI Appendix*, Table S2). (*B*) Frequency distribution of oyster size classes by time period. (*C*) Oyster shell showing location of the height measurement.

and the formation of the modern-day Chesapeake Bay (10, 19). Due to sea-level rise, preservation conditions, and a dearth of research, only a few shell middens—archaeological trash deposits with shellfish and other materials—are known to date to before about 3,200 y ago. In contrast, middens younger than 1,500 y old are common and provide a record of human interaction with the Chesapeake Bay before European colonization (20–22). Previous studies of past Chesapeake oyster populations include estimates of reef accretion rates (17, 23), analysis of how historical nutrient input may have resulted in larger oyster sizes (21), evidence for colonial-period drought and higher estuarine salinity (24), changes in oyster growth rates from late prehistoric to modern times (25), and the possibility of localized overharvest during the colonial period (9, 20). However, there has been limited investigation into prehistoric Native American impact on Chesapeake Bay oysters, with previous studies limited to a single site or localized area (26, 27).

We explore prehistoric (late Holocene; ∼3,500–400 y ago) changes in Chesapeake Bay oysters within the context of broad trends from the Pleistocene to the Anthropocene, using a massive dataset of measurements of 47,927 archaeological (prehistoric/historic; $n = 24{,}085$), fossil (Pleistocene; $n = 621$), and modern ($n = 23{,}221$) oysters (Fig. 1). Archaeologists around the world have used size changes in mollusks as indicators of human overharvest, sustainability, and other variables (28–30). Our study is the first, to our knowledge, to integrate paleontological, prehistoric/historic archaeological, and modern (A.D. 2000–2014) oyster size data to understand the evolution of a fishery over some 300,000 y before human colonization and across a range of human occupations. These data to our knowledge also provide the first comprehensive millennial-scale and bay-wide analysis of the Chesapeake oyster fishery before overfishing, introduced oyster diseases, and eutrophication that have shaped oyster populations for the past 150 y.

Shellfish size is a metric commonly used to understand human impacts on fisheries, but other factors such as abundance and demographic data (e.g., age) are often used in modern studies. We focus on size because it is currently the only metric that can be standardized across the samples and time periods of interest. Moreover, size is the metric used to regulate the fishery today (minimum catch size >76 mm). Some researchers have speculated that Native American harvest pressure on oysters was minimal (10), and there are anecdotal accounts of extremely large (1-ft) oysters in historical times (6). Therefore, we predicted that our bay-wide prehistoric archaeological data would contain a mix of oyster sizes, including very large specimens similar to Pleistocene samples before human harvest. We expected archaeological samples to be skewed toward larger sizes relative to today, with any widespread size reduction occurring late in the prehistoric period or during colonial and historic times. We also hypothesized that there would be some prehistoric size reduction through time indicative of human harvest pressure, because archaeological studies have shown that ancient peoples all over the world had an influence on shellfish size (28–30). Alternatively, an absence of size declines and no change in oyster relative abundance would suggest that the oyster fishery was sustainable over the long term. We also explored alternative hypotheses, including human food preferences and the effects of changing physical and biotic conditions.

Results

Oyster data were grouped for three different scales of analysis. At the first scale, we use broad temporal and spatial categories to explore changes and potential human impacts on oysters through time and throughout the entire Chesapeake (bay-wide). Within this broadest scale, we divided our data into Pleistocene (0.781 Ma to 13,000 y ago), prehistoric (3,200–400 y ago), historic (400–50 y ago), and modern (A.D. 2000–2014) categories. Still at the broad Chesapeake scale, we then subdivided the data into middle (0.781–0.126 Ma) and late Pleistocene (0.126 Ma to 13,000 y ago), Early (3,200–2,500 y ago), Middle (2,500–1,100 y ago), and Late Woodland (1,100–400 y ago), historic (including the colonial period, 400–50 y ago), and modern upper Chesapeake Bay, lower Chesapeake Bay, and Virginia coastal bays (A.D. 2000–2014). The second scale of analysis is smaller, providing a detailed examination of archaeological investigations in two watersheds—Fishing Bay and Rhode River. The third scale of analysis quantified oyster size changes within single archaeological sites.

Oyster Size Through Time. Our proxy for oyster size is measurement of oyster height (>35 mm). This analysis yielded a wide range of oyster sizes, including oysters as large as 259 mm in the Pleistocene, 189 mm in the prehistoric, and 156–157 mm in historic and modern times (Fig. 1 and *SI Appendix*, Tables S1 and S2). A Kruskal–Wallis test followed by post hoc Mann–Whitney *U* tests showed that there are some significant differences in oyster height through time ($X^2 = 1613.7$, $P < 0.01$) (*SI Appendix*, Tables S3–S14). The largest reduction (17%; Mann–Whitney *U* 2,403,646, effect size 0.58, $P < 0.01$) in oyster height was from the Pleistocene (mean 87 mm, SD 38.7, $n = 621$) to the prehistoric (mean 72 mm, SD 20.1, $n = 6{,}648$) assemblages. There is no statistically significant difference between middle Pleistocene (mean 92 mm, SD 28.0, $n = 36$) and late Pleistocene oyster height (mean 86 mm, SD 39.3, $n = 585$), but between the late Pleistocene and Early Woodland (mean 61 mm, SD 14.8, $n = 469$) there is a significant decrease in oyster height. Oyster size increases significantly between the Early and Middle Woodland (mean 70 mm, SD 19.9, $n = 571$) and again between the Middle and Late Woodland (mean 74 mm, SD 20.2, $n = 5{,}608$). Compared with Late Woodland oysters, historic (mean 81 mm, SD 20.1, $n = 198$) oysters are significantly larger. Modern oysters (mean 72 mm, SD 19.7, $n = 23{,}221$) are significantly smaller than historic oysters. Rather than decreasing through time with greater human harvest, harvested oysters tend to get larger through the late Holocene (prehistoric/historic) until modern size declines, but all oyster averages during the Holocene are smaller than Pleistocene samples.

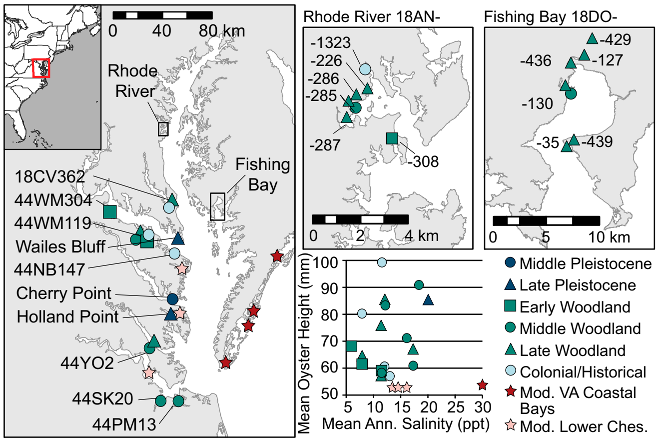

Fig. 2. Location of sites in this study, with the mean oyster height of each site plotted against the mean salinity known for those areas today and estimated for the Pleistocene samples. The modern upper Chesapeake oysters come from dozens of upper bay sampling sites, and consequently these are not shown on the map. Modern mean annual salinity is plotted against average oyster height for each archaeological and modern site. Pearson's correlation coefficient values show weak correlation between size and estimated salinity (*SI Appendix*, Table S16). ppt, parts per thousand.

Oyster size distributions show differences between human-selected and natural oyster assemblages by time period (Fig. 1). Kolmogorov–Smirnov tests detected significant differences in all pairwise comparisons in oyster size distributions between the Pleistocene, prehistoric, historic, and two modern assemblages (*SI Appendix*, Table S15). Oyster height in the Pleistocene fossil reef assemblage has a larger SD (38.7 mm) and is heavily positively skewed (more individuals in smaller size classes) compared with Holocene archaeological assemblages (prehistoric SD 20.1 mm, historic SD 20.1 mm). Modern oyster reefs from the outer Virginia coastal bays and the upper Chesapeake also have significantly different population distributions from either Pleistocene reefs or archaeological sites, according to Kolmogorov–Smirnov tests (*SI Appendix*, Table S15). Although it cannot be compared statistically (*Materials and Methods*), the modern sample from the lower Chesapeake appears to be similar to the sample from the outer Virginia coastal bays (Fig. 1). Like the Pleistocene reef samples, the lower Chesapeake and Virginia coastal bay modern reef samples are heavily positively skewed, but the modern reefs have narrow SDs and are lacking the very large size classes present in the Pleistocene, probably due to modern overharvest and disease.

A scatterplot of our samples based on known (modern) or estimated (Pleistocene, prehistoric, and historic) salinity shows no clear temporal or spatial patterns between salinity and oyster size at the bay-wide level (Fig. 2). Analysis of correlation and linear regression shows little relationship between oyster size and the salinity estimates or distance to the mouth of the bay (*SI Appendix*, Table S16). There is a weak positive correlation between modern mean annual salinity and oyster height at prehistoric archaeological sites at the bay-wide level (Pearson's $r = 0.403$, $P = 0.063$), but the r^2 value (0.16) suggests that most of the variation in oyster height bay-wide cannot be explained solely by salinity.

Prehistoric Human Impacts on Oysters. Analysis of oysters from archaeological sites in two Maryland watersheds (Fishing Bay and the Rhode River) supply detailed patterns for individual watersheds across 3,200–1,500 y of Native American harvest (Fig. 3). In the Rhode River, there is statistical support (*SI Appendix*, Tables S7 and S8) for significant differences in size between most pairs of archaeological sites, but they do not decrease through time, as we would expect if humans were overharvesting this ecosystem. There is a statistically significant increase in size (14–20 mm) during the historic-period occupation at 18AN1323 (Fig. 3 and *SI Appendix*, Tables S13 and S14). At Fishing Bay, only one site, 18DO439, had a significantly different oyster assemblage (larger average size) from all other sites. This site overlaps temporally with 18DO429 and 18DO436, suggesting that the size difference could result from harvesting different microenvironments.

The potential impact of environmental variables becomes clearer when we compare our high-resolution datasets from the Rhode River and Fishing Bay with each other (Fig. 3). When all samples within each watershed are aggregated, oyster size differences between watersheds are statistically significant (Mann–Whitney U 2,869,300, $P < 0.01$), with larger oysters (mean 84 mm, SD 21.9 mm, $n = 2{,}619$) in the higher salinity of Fishing Bay and smaller oysters (mean 66 mm, SD 15.5 mm, $n = 4{,}227$) in the lower salinity of the Rhode River. There is a strong positive correlation between oyster size and modern salinity (Pearson's $r = 0.806$, $P < 0.001$) at these 12 archaeological sites. An r^2 value of 0.647 suggests that salinity is a moderately good predictor of oyster height in individual watersheds but that other factors are also important.

Four sites (18DO429 and 18DO439 at Fishing Bay and 18AN285 and 18AN1323 in the Rhode River) provide a good stratigraphic control to test whether there may have been short-term human impact on oyster size by people occupying the same location (Fig. 4). Kruskal–Wallis tests showed no statistically significant differences in oyster populations through time at either of the Fishing Bay sites, 18DO429 ($X^2 = 1.20$, $P = 0.27$, $n = 51$) or 18DO439 ($X^2 = 3.82$, $P = 0.28$, $n = 119$), but the samples are relatively small. At site 18AN285 in the Rhode River, Kruskal–Wallis and post hoc Mann–Whitney U tests showed statistically significant differences ($X^2 = 41.18$, $P < 0.01$, $n = 1{,}176$) in size between level 4 and levels 5–7, which might be from harvesting different microenvironments or environmental variability. There are no statistically significant pairwise comparisons between levels in the other Rhode River site, 18AN1323. Finally, an abundance index that measures human prey selectivity and compares oyster relative abundance with all other shellfish identified in each of the Fishing Bay and Rhode River shell middens demonstrates that oysters make up over 90% of all shellfish at each of the archaeological sites, with no decline in relative abundance through time (*SI Appendix*, Fig. S1).

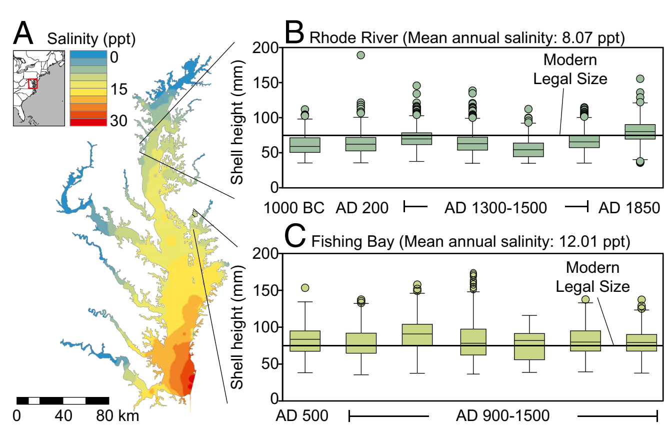

Fig. 3. Changes in oyster height from archaeological sites in specific watersheds in Chesapeake Bay. (*A*) Average annual salinity from 2000 to 2014 (data from the Chesapeake Bay Program Water Quality Database, www.chesapeakebay.net/data/downloads/cbp_water_quality_database_1984_present, accessed May 8, 2015). (*B* and *C*) Oyster height from archaeological sites in the Rhode River, Maryland (*B*) and Fishing Bay, Maryland (*C*). See the legend for Fig. 1 for a description of the box-and-whisker plots. ppt, parts per thousand.

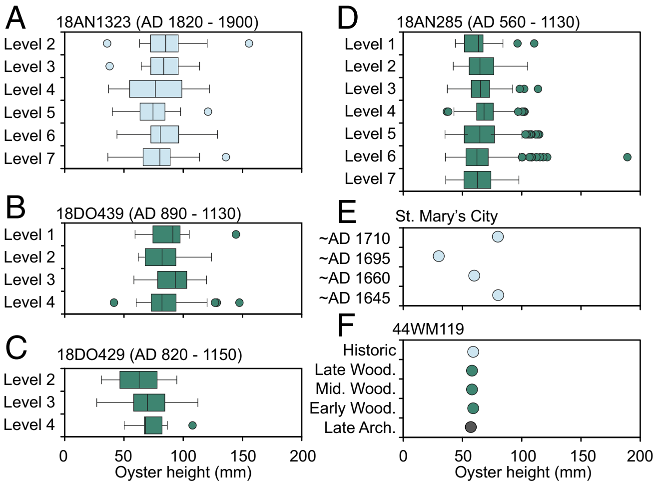

Fig. 4. Oyster size variation through time within archaeological sites in the Chesapeake Bay. (*A*–*D*) Oyster height through time from individual archaeological samples in the Rhode River and Fishing Bay study areas, with the bottom (oldest) to the top (youngest). (See the legend for Fig. 1 for an explanation of the box-and-whisker plots.) (*E*) Mean oyster height through time at a historic site complex (St. Mary's City) (9). (*F*) Mean oyster height at a large shell midden near the Potomac River, Virginia (44WM119) (26).

Discussion

Pleistocene-to-Anthropocene Oysters. This study of a long-term record of oyster size changes, comparing archaeological, Pleistocene fossil, and modern oysters, provides to our knowledge the first bay-wide, millennial-scale window into human harvest of Chesapeake oysters, serving as a model for future research elsewhere around the world. These data do not fully support our predictions about the effects of Native American harvest on oysters. Prehistoric archaeological oyster sizes do vary through time but are generally smaller than Pleistocene oysters, and there is no evidence for a systematic size reduction during prehistoric human occupation (~3,500–400 y ago). At the bay-wide scale, oysters actually demonstrate an increase in size through time. No single environmental or cultural variable explains this increase, it does not occur within individual watersheds or at single sites, and we caution that our Early Woodland sample comes primarily from the lower salinity waters of Rhode River, and oyster sizes may be smaller as a result.

The size data from the Pleistocene reefs compared with later archaeological and modern samples demonstrate differences in population structure between cultural and natural accumulations of Chesapeake oysters, with more oysters in smaller size classes in the natural accumulations. These differences are not a result of our sampling for this study, because similar bulk sampling methods were used for nonmodern materials and similar random samples were used for the modern samples. We believe this likely reflects the human-selected (e.g., hand-collected) nature of the prehistoric archaeological oysters, which could have resulted in more consistent average sizes and fewer very small individuals. People were likely removing oysters from the reefs in a way that was biased toward medium-sized oysters, but there were no major decreases in mean oyster height during the prehistoric Native American occupation (3,500–400 y ago). It is unclear why the largest size classes present in the unfished Pleistocene samples were not documented in the archaeological samples. It is unlikely that these are solely a result of differing paleoenvironmental conditions, because salinity and temperature ranges for the three Pleistocene (or fossil) sites fall within ranges observed from Delaware to North Carolina today (*SI Appendix*, *SI Text*). It is possible that these largest oysters were overharvested by Native Americans before 3,500 y ago, but earlier human populations were small and only a handful of shell middens pre-dating 3,500 y ago are known to exist. Alternatively, many of the largest oysters could have lived in deeper waters that were not generally harvested by Native Americans. Another possibility is that people were choosing not to harvest the largest oysters.

Comparison of modern oyster populations with either the human-selected archaeological and historical samples or the Pleistocene oyster deposits is challenging, because nutrient pollution, disease, and intensive harvest pressure have combined to reduce recruitment in modern Maryland waters and to differentially kill off larger oysters both in Maryland and Virginia (13, 15). There are similarities between size distributions in Pleistocene Chesapeake Bay oyster populations and those along the modern Virginia coastal bays and lower Chesapeake Bay, but very large oysters (>150 mm) were more common in the Pleistocene. This could be due to the fact that modern diseases kill oysters before they reach those large sizes and that fishing regulations permit harvest of larger individuals (>76 mm) within the populations. The modern data from the upper Chesapeake Bay (Maryland) are an outlier among the modern assemblages, containing larger average sizes driven by a general dearth of small oyster size classes (35–50 mm), because the population experiences infrequent and irregular recruitment. Although dramatically reduced in number and recruitment [e.g., <1% of historical abundance (13)], Maryland oysters are still achieving average sizes comparable to those harvested in prehistoric times during the past 3,000 y. We caution that this may be due primarily to the absence of individuals in small size classes rather than growth rates comparable to those in the prehistoric period. The similarities between these two datasets may be coincidental, and require additional analysis.

Environmental Variables and Oyster Size. Oyster size and abundance are products of the environmental conditions in which they live, and human harvest cannot be understood without also considering the potential influence of environmental change. Salinity is a driving factor for oyster size in both ancient and modern times, and influenced the size of oysters harvested by Native Americans in local watersheds (Fig. 3 and *SI Appendix*, Table S16). However, when viewed from the perspective of the entire bay, the correlation between salinity and oyster size is relatively weak (Fig. 2). This could result from the high geographic and temporal variability in Chesapeake salinity, which is difficult to sample at a single archaeological site with broad temporal and spatial resolution that could obscure expected variability. Despite the limited correlation between salinity and oyster size bay-wide, there is a size–salinity correlation in two individual watersheds.

Longer-term climate patterns influenced regional paleoenvironmental conditions but do not appear to have significantly influenced Native American oyster harvest. The Chesapeake region responded to the Medieval Climatic Anomaly, with warm, dry atmospheric conditions and higher salinity and higher water temperatures between A.D. 400 and 900 and cool, wet atmospheric conditions and cool, less saline water conditions between A.D. 1050 and 1750 (31, 32). Relative sea level in the Chesapeake Bay has continued to rise throughout the past 3,500 y due to the collapse of the Laurentide ice sheet forebulge, with ~7 m of relative sea-level rise during that period (33). Our data suggest that these major shifts had little effect on prehistoric harvest patterns, at least on archaeological timescales, but they warrant more detailed study.

Nutrients and sedimentation are also drivers of oyster productivity, and likely influenced oyster populations during the historic period. A 2,000-y study of Chesapeake nutrients and eutrophication demonstrates important increases during the historic and modern periods, likely associated with landscape clearing for agriculture and increased sedimentation in the historic and modern periods, but suggests little change throughout Native American occupation (34). These historic nutrient increases likely influenced the size increase we noted in historic-period Rhode River oysters, which was similar to a pattern identified in the St. Mary's and Patuxent rivers (21). Together, these data suggest that human activities, biotic conditions, and climatic variability likely worked in concert to influence long-term oyster productivity, size, and abundance.

Sustainability of the Native American Fishery. With limited variability in oyster size and abundance and no systematic evidence for a size decline through time during the period from 3,500 to 400 y ago, the Native American Chesapeake Bay oyster fishery appears to have been largely sustainable. A variety of factors may help explain this, including technological limitations that resulted in primarily nearshore harvest, seasonal rounds where people only exploited oysters during a particular time of year, low human population density, and broad-spectrum human diets that incorporated a mix of marine and terrestrial resources and cultigens. Little is known about the precise methods that prehistoric Native Americans used to obtain oysters, but hand collection—perhaps using simple tools in relatively shallow water—was likely the most common method (20). Hand collection of oysters in nearshore, shallow-water/fringing reefs may have promoted consistent size classes in middens, and may have left significant oyster populations in deeper water free from human harvest. This would have limited the long-term impacts on regional oyster populations by preserving a source population to supply recruits and by leaving substantial portions of the hard substrate and/or overall 3D reef structure intact. Native Americans in the Chesapeake are known to have harvested a wide variety of marine and terrestrial foods, with evidence for maize cultivation, especially on the major western-shore drainages, beginning ~1,000 y ago (10). These diverse subsistence strategies would have reduced pressure on single-resource classes (i.e., oysters), and may have further helped oyster recruitment following significant Native American harvest. Although there are many details of Native American harvest of oysters that remain unknown, we do know that, in contrast to historic and modern times, Native American population densities were much lower, there was no significant trade of oysters outside of the Chesapeake region, oyster shell was generally not mined for construction, and harvest methods were far less destructive than historic and modern techniques [e.g., dredging with sail and steam boats (8)].

Although our study is the first, to our knowledge, to analyze oyster size throughout the Chesapeake Bay, a few archaeological studies have investigated past oyster size at single sites or localized areas (9, 26, 27). Data from the White Oak Point site in Virginia provide the longest sequence from a single site in the region. Evidence at White Oak Point from ~4,500 y ago through the early historic period supports our findings, suggesting continuity in oyster size (Fig. 4) (26). The St. Mary's City site in Maryland provides evidence for a localized size decline from the 16th to 17th centuries that was associated with human population growth during the colonial period (9, 20). Additional research has suggested that this decline may have been followed by 19th-century size increases, perhaps associated with eutrophication and higher nutrient load that increased oyster growth rates (21). When considered alongside the prehistoric dataset presented here, the historic period shows collection of larger oyster size in the Chesapeake. We attribute this to technological shifts, including the introduction of tonging in the 18th century followed by dredging in the 19th century (9, 10, 12, 20), which may have increased access to larger oyster size classes from deeper waters that were previously not harvested by Native Americans. Increased nutrient load likely also played a role, but this needs additional testing (21).

Other aspects of human behavior may have contributed to the apparent sustainability observed in the Native American size data. One possibility is that Native Americans preferred medium-sized oysters or lacked the technology to open larger oysters. Although food preferences may have played a role in the sizes present in our data, the presence of both small and larger individuals suggests a wide range of oysters were harvested. We reject the notion that Native Americans lacked the technology to process larger oysters. These could be broken with a hammerstone or opened with heat, like other sizes. Similarly, salinity, nutrients, and other variables influenced oyster size, particularly in local catchments, but none show a clear correlation with the patterns we observe bay-wide. Collectively, the archaeological size and abundance data suggest that the most parsimonious explanation is that the Native American fishery was sustainable at century and millennial timescales. This does not mean that Native Americans did not have distinct temporal or localized impacts on local reefs. However, harvest patterns reveal no systematic decline in size or abundance like those observed by archaeologists in other parts of the world (28–30).

Elsewhere in North America, analyses of late Holocene *Crassostrea virginica* from Florida (35) and New York's Hudson River estuary (36) also document continuity in oyster size and no prehistoric size declines. Analysis of shell rings in the southeastern United States suggests a mix of human influence, with some arguing for significant human impact (37) and others for more limited effects (38). Beyond North America, analysis of *Ostrea edulis* in Denmark demonstrates human-induced size decreases from the Mesolithic to the Neolithic (39). Together, these data demonstrate a range of human influence on oyster size in the past but general resilience to Native American harvest pressure in several North American *C. virginica* populations. These data add to a growing body of research around the world that documents a continuum of ancient human influence on shellfish populations, ranging from human-induced reduction of shellfish size from overexploitation to continuity and size increases that may have resulted from changing environmental variables, especially nutrient increases (26–30, 35–40).

Implications for the Anthropocene. The modern Chesapeake Bay, like other estuaries around the world, is a complicated system where recovery is hindered by an array of factors. Oysters are currently combating the sustained effects of overfishing, introduced and native disease [multinucleated sphere unknown (MSX) and *Perkinsus marinus* (dermo)], climate change, eutrophication, and sedimentation, some of which were not major drivers of change in past ecosystems (11, 41, 42). Although many of these did not play a major role in the prehistoric oyster fishery, our research demonstrates the resilience of oyster populations through rising sea levels, changing climate, and extensive Native American harvest over several millennia.

This model of a sustainable prehistoric Native American harvest of oysters, primarily by hand collecting from fringing reefs that left deeper-water reefs largely intact, provides insight into modern restoration. Although the effectiveness of the modern restoration strategy of Chesapeake oysters is debated (5, 15), our Pleistocene-to-Anthropocene size and archaeological relative abundance data provide some support for recent Chesapeake Bay oyster restoration efforts, including reduction of modern harvest levels and creation of increased no-take zones (13, 43) that would mimic the more mobile and flexible Native American fishery. Current restoration plans (44) include enhancement of oyster density using hatchery seed, addition of new hard substrate where needed, and no-take reserves that are conceptually similar to deep-water areas where harvest was unlikely before the introduction of oyster tongs and dredges. In addition, our Pleistocene data provide a baseline against which the size distribution of oysters in no-take reserves could be evaluated. These data do not provide all of the answers to a very challenging and complicated restoration and conservation effort, but they do provide an example of an apparently sustainable millennial-scale fishery, elements of which may help inform restoration and harvest in today's ecosystem.

Finally, our data illustrate the importance of conserving oysters beyond the ecological services or food they provide. Eastern oysters, like other oysters around the world, are deeply intertwined with the people who lived around the Chesapeake Bay and beyond (7, 10). Consequently, oysters warrant conservation for their significant role in North American cultural history, including that of Native Americans, Euro-American colonists, modern watermen, and the general public.

Materials and Methods

We reconstructed the size of *C. virginica* using measurements of whole left oyster valve height from archaeological and fossil contexts and modern reef sites (*SI Appendix, SI Text*). Height (also called length) is the greatest dimension in millimeters from the hinge to the growth edge (Fig. 1). We excluded specimens that were smaller than 35 mm from our analysis because some of the modern datasets do not include juveniles/spat. Although this results in slight increases in average sizes (1 mm or less), this had no effect on our interpretations and makes our data comparable across time periods.

We synthesized previously reported values for archaeological oyster mean size, which did not exclude oysters smaller than 35 mm (*SI Appendix*, Table S2). All measurements are derived from well-dated archaeological and fossil contexts, with ages based on radiocarbon dates and time-sensitive artifacts for archaeological assemblages and on amino acid racemization and stratigraphic relationships for the fossil assemblages (*SI Appendix*, Tables S1, S2, S18, and S19). Modern samples are from stratified random stock assessment surveys, providing a range of environmental conditions for comparison (*SI Appendix, SI Text*).

Statistical analysis of all samples in *SI Appendix*, Table S1 was performed in R version 3.2.3 (*SI Appendix, SI Text*). Modern samples from the lower Chesapeake Bay were included in most of our study but excluded from some statistical analyses because oyster size data were only available in categorical bins (1–2 mm, 5–6 mm, etc.) rather than raw data. We compare oyster height with estimated salinity and distance to the mouth of the Chesapeake because environmental factors (salinity, nutrients, dissolved oxygen, etc.) vary with distance to mouth within watersheds (45). Because previous studies of Chesapeake Bay nutrient and sediment load (34) were on different temporal and spatial scales from our data, we make qualitative rather than statistical comparisons. We also analyzed archaeological data from oysters from small subestuaries, where environmental conditions were less likely to vary spatially at a specific time interval (46).

ACKNOWLEDGMENTS. We thank numerous students and colleagues for helping to obtain and measure the oysters presented in our analysis and Krithi Sankaranarayanan for help with statistical analyses. M. Tarnowski (Maryland DNR) provided the modern Maryland data. Our archaeological research was supported by the National Geographic Society (CRE 8960-11) and the Smithsonian Institution.

1. Jackson JBC, et al. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293(5530):629–637.
2. Lotze HK, et al. (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312(5781):1806–1809.
3. Beck MW, et al. (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *BioScience* 61(2):107–116.
4. Grabowski JH, et al. (2012) Economic valuation of ecosystem services provided by oyster reefs. *BioScience* 62(10):900–909.
5. Lipcius RM, et al. (2015) Overcoming restoration paradigms: Value of the historical record and metapopulation dynamics in native oyster restoration. *Front Mar Sci* 2:65.
6. Zu Ermgassen PSE, et al. (2012) Historical ecology with real numbers: Past and present extent and biomass of an imperilled estuarine habitat. *Proc Biol Sci* 279(1742):3393–3400.
7. Keiner C (2009) *The Oyster Question: Scientists, Watermen, and the Maryland Chesapeake Bay Since 1880* (Univ of Georgia Press, Athens, GA).
8. Lotze HK (2010) Historical reconstruction of human-induced changes in US estuaries. *Oceanogr Mar Biol* 48:267–338.
9. Miller HM (1986) Transforming a "splendid and delightsome land": Colonists and ecological change in the Chesapeake 1607–1820. *J Wash Acad Sci* 76(3):173–187.
10. Miller HM (2001) Living along the "Great Shellfish Bay": The relationship between prehistoric peoples and the Chesapeake. *Discovering the Chesapeake: The History of an Ecosystem*, eds Curtin PD, Brush GS, Fisher GW (Johns Hopkins Univ Press, Baltimore), pp 109–126.
11. Rothschild BJ, Ault JS, Goulletquer P, Héral M (1994) Decline of the Chesapeake Bay oyster population: A century of habitat destruction and overfishing. *Mar Ecol Prog Ser* 111:29–39.
12. Kirby MX (2004) Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. *Proc Natl Acad Sci USA* 101(35):13096–13099.
13. Wilberg MJ, Livings ME, Barkman JS, Morris BT, Robinson JM (2011) Overfishing, disease, habitat loss, and potential extirpation of oysters in upper Chesapeake Bay. *Mar Ecol Prog Ser* 436:131–144.
14. Schulte DM, Burke RP, Lipcius RN (2009) Unprecedented restoration of a native oyster metapopulation. *Science* 325(5944):1124–1128.
15. Mann R, Powell EN (2007) Why oyster restoration goals in the Chesapeake Bay are not and probably cannot be achieved. *J Shellfish Res* 26(4):905–917.
16. Wharton J (1957) *The Bounty of the Chesapeake: Fishing in Colonial Virginia* (Virginia 350th Anniversary Celebration, Williamsburg, VA).
17. Mann R, Harding JM, Southworth MJ (2009) Reconstructing pre-colonial oyster demographics in the Chesapeake Bay, USA. *Estuar Coast Shelf Sci* 85(2):217–222.
18. Newell R (1988) Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica? Understanding the Estuary: Advances in Chesapeake Bay Research*, eds Lynch MP, Krone EC CRC Publication (Chesapeake Bay Res Consort, Solomons, MD), Vol 129, pp 536–546.
19. Bratton JF, Colman SM, Thieler ER, Seal RR, II (2003) Birth of the modern Chesapeake Bay estuary between 7.4 and 8.2 ka and implications for global sea-level rise. *Geo-Mar Lett* 22(4):188–197.
20. Kent BW (1992) *Making Dead Oysters Talk: Techniques for Analyzing Oysters from Archaeological Sites* (Maryland Hist Trust, Crownsville, MD).
21. Kirby MX, Miller HM (2005) Response of a benthic suspension feeder (*Crassostrea virginica* Gmelin) to three centuries of anthropogenic eutrophication in Chesapeake Bay. *Estuar Coast Shelf Sci* 62(4):679–689.
22. Rick TC, Lockwood R (2013) Integrating paleobiology, archeology, and history to inform biological conservation. *Conserv Biol* 27(1):45–54.
23. DeAlteris JT (1988) The geomorphic development of Wreck Shoal, a subtidal oyster reef of the James River, Virginia. *Estuaries Coasts* 11(4):240–249.
24. Harding JM, Spero HJ, Mann R, Herbert GS, Sliko JL (2010) Reconstructing early 17th century estuarine drought conditions from Jamestown oysters. *Proc Natl Acad Sci USA* 107(23):10549–10554.
25. Harding JM, Mann R, Southworth MJ (2008) Shell length-at-age relationships in James River, Virgina, oysters (*Crassostrea virginica*) collected four centuries apart. *J Shellfish Res* 27(5):1109–1116.
26. Waselkov GA (1982) *Shellfish Gathering and Shell Midden Archaeology*. PhD dissertation (University of North Carolina, Chapel Hill, NC).
27. Jenkins JA (2013) Truly long-term sustainability: An archaeological analysis of oyster shell. The 3rd World Sustainability Forum. Available at sciforum.net/conference/wsf3.
28. Klein RG, Steele TE (2013) Archaeological shellfish size and later human evolution in Africa. *Proc Natl Acad Sci USA* 110(27):10910–10915.
29. Erlandson JM, Rick TC, Braje TJ, Steinberg A, Vellanoweth RL (2008) Human impacts on ancient shellfish: A 10,000 year record from San Miguel Island, California. *J Archaeol Sci* 35(8):2144–2152.
30. Thomas KD (2015) Molluscs emergent, Part II: Themes and trends in the scientific investigation of molluscs and their shells as past human resources. *J Archaeol Sci* 56:159–167.
31. Cronin TM, et al. (2010) The Medieval Climate Anomaly and Little Ice Age in Chesapeake Bay and the North Atlantic Ocean. *Palaeogeogr Palaeoclimatol Palaeoecol* 297(2):299–310.
32. Willard DA, Cronin TM, Verardo S (2003) Late-Holocene climate and ecosystem history from Chesapeake Bay sediment cores, USA. *Holocene* 13(2):201–214.
33. Engelhart SE, Horton BP, Douglas BC, Peltier WR, Törnqvist TE (2009) Spatial variability of late Holocene and 20th century sea-level rise along the Atlantic coast of the United States. *Geology* 37(12):1115–1118.
34. Cooper SR, Brush GS (1993) A 2,500-year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries Coasts* 16(3):617–626.
35. Sampson CP (2015) Oyster demographics and the creation of coastal monuments at Roberts Island Mound Complex, Florida. *Southeast Archaeol* 34(1):84–94.
36. Claassen C, Whyte T (1995) Biological remains at Dogan Point. *Dogan Point: A Shell Matrix Site in the Lower Hudson Valley*, ed Claassen C (Occasional Publications Northeastern Anthropol, Bethlehem, PA), pp 65–78.
37. Dame RF (2009) Shifting through time: Oysters and shell rings in past and present southeastern estuaries. *J Shellfish Res* 28(3):425–430.
38. Doucet JA (2012) *Oysters and Catfish: Resource Exploitation at Rollins Shell Ring, Ft. George Island, Florida*. Master's thesis (Louisiana State University, Baton Rouge, LA).
39. Milner N (2013) Human impacts on oyster resources at the Mesolithic-Neolithic transition in Denmark. *The Archaeology and Historical Ecology of Small-Scale Economies*, eds Thompson VD, Waggoner JC, Jr (Univ Press of Florida, Gainesville, FL), pp 17–40.
40. Giovas CM, Clark M, Fitzpatrick SM, Stone J (2013) Intensifying collection and size increase of the tessellated nerite snail (*Nerita tessellata*) at the Coconut Walk site, Nevis, northern Lesser Antilles, AD 890–1440. *J Archaeol Sci* 40(11):4024–4038.
41. Luckenbach M, Mann R, Wesson J, eds (1999) *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches* (Virginia Inst Marine Sci, Gloucester Point, VA).
42. Mann R (2000) Restoring the oyster reef communities in Chesapeake Bay: A commentary. *J Shellfish Res* 19(1):335–339.
43. Breitburg DL, et al. (2000) Oyster reef restoration: Convergence of harvest and conservation strategies. *J Shellfish Res* 19(1):371–377.
44. US Army Corps of Engineers (2012) *Chesapeake Bay Oyster Recovery: Native Oyster Restoration Management Plan* (US Army Corps of Engineers, Baltimore, MD).
45. Kuo AY, Park K, Moustafa MZ (1991) Spatial and temporal variabilities of hypoxia in the Rappahannock River, Virginia. *Estuaries Coasts* 14(2):113–121.
46. Mann R, Southworth M, Harding JM, Wesson JA (2009) Population studies of the native Eastern oyster, *Crassostrea virginica*, (Gmelin, 1791) in the James River, Virginia, USA. *J Shellfish Res* 28(2):193–220.