ANTHROPOLOGY

Ecosystem stability and Native American oyster harvesting along the Atlantic Coast of the United States

Victor D. Thompson[1]*, Torben Rick[2], Carey J. Garland[1], David Hurst Thomas[3], Karen Y. Smith[4,5], Sarah Bergh[6], Matt Sanger[7], Bryan Tucker[8], Isabelle Lulewicz[1], Anna M. Semon[3], John Schalles[9], Christine Hladik[10], Clark Alexander[11], Brandon T. Ritchison[12]

The eastern oyster (*Crassostrea virginica*) is an important proxy for examining historical trajectories of coastal ecosystems. Measurement of ~40,000 oyster shells from archaeological sites along the Atlantic Coast of the United States provides a long-term record of oyster abundance and size. The data demonstrate increases in oyster size across time and a nonrandom pattern in their distributions across sites. We attribute this variation to processes related to Native American fishing rights and environmental variability. Mean oyster length is correlated with total oyster bed length within foraging radii (5 and 10 km) as mapped in 1889 and 1890. These data demonstrate the stability of oyster reefs despite different population densities and environmental shifts and have implications for oyster reef restoration in an age of global climate change.

INTRODUCTION

Anthropologists and historians are increasingly critical of the long-held and widely shared view of non-European peoples as isolated entities before the advent of European colonialism. This perspective is rooted in the mistaken assumption that indigenous people and their institutions were unchanging, as the noted anthropologist Wolf put it: "people without history" (*1*). Here, we argue that increasingly fine-grained archaeology, paleobiology, and 19th century cartography provide a deep history that can inform biological conservation by providing critical historical baselines that document the processes responsible for ongoing changes in coastal ecosystems, including the collapse of fisheries (*2*).

Identifying the core social and environmental processes responsible for resource depletion is critical for management decisions regarding particular resources or attempts at ecosystem restoration. Oysters (Ostreidae) are valuable proxies for past human-induced and ecological change (*2*) and, along with other mollusks, have been used by some as a marker of the Anthropocene (*3*). However, if we rely on keystone species like oysters as proxies for investigating historical trajectories of past ecosystems, it is critical to understand the social and environmental factors that condition their productivity at both local and regional scales across long periods.

Thus, we explore the deep history of harvesting eastern oysters (*Crassostrea virginica*) in the American South to investigate the structure of oyster reef ecosystems from initial human harvesting to the modern era, i.e., from the early Late Archaic [ca. 4500 to 3500 calibrated years before the present (cal. BP)], the Mississippian period (ca. 1000 to 500 cal. BP), and into the late 1800s and 1970s. Tracking changes in oyster size provides insight into the health of reefs, as shifts in size have been directly correlated to environmental change, including human predation (*4*, *5*). Specifically, the size of oysters and the main drivers of their ecology are determined by the age of the animal, environmental variability, ontogenetic growth rates, and the structure of the reef and the oyster's location within it (*6*, *7*). Therefore, large samples from multiple sites are needed to evaluate shifts in oyster paleobiology. Understanding these past dynamics can help prepare for future oyster reef ecosystem management. We focus on four interrelated questions: (i) Did oyster size vary from the Late Archaic to the Mississippian periods into the 1800s (a roughly 5000-year period of intensive harvest)? (ii) Did oyster size vary latitudinally across the southeastern United States? (iii) To what extent are observed variations in oyster size across space and time linked to environmental and social drivers? (iv) How can such historical and paleobiological studies inform modern restoration and conservation of oyster fisheries?

The Georgia Bight extends from present-day South Carolina to northern Florida along the Atlantic coast of the United States and is home to some of the most productive estuaries in the world (Fig. 1) (*8*). These estuaries have undergone and continue to experience marked changes due to human exploitation and climate change. The harvesting of eastern oysters as a food resource and possible building material began along the Georgia Bight almost 5000 years ago. Oysters and other coastal species continue to be commercially harvested from the region, raising increased concerns for sustainable management (*9*). Here, we use three different datasets to examine the long-term stability/resilience in oyster fisheries over time and how social factors and environmental changes affected these fisheries. These include oyster measurements ($n = 37{,}805$) from archaeological sites dated to two critical periods with different modes of food production: the Late Archaic (ca. 4500 to 3500 cal. BP) and the Mississippian period (ca. 1000 to 500 cal. BP), as well as the distribution of oyster beds as mapped in the late 1800s (and again in the 1970s). These data reveal long-term temporal trends in oyster sizes and latitudinal

[1]University of Georgia, Department of Anthropology, 250A Baldwin Hall, Athens, GA 30602, USA. [2]Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA. [3]American Museum of Natural History, Division of Anthropology, 79th Street at Central Park West, New York, NY 10024, USA. [4]South Carolina Department of Natural Resources, 1000 Assembly Street, Columbia, SC 29201, USA. [5]South Carolina Institute of Archaeology and Anthropology, University of South Carolina, 1321 Pendleton Street, Columbia, SC 29208, USA. [6]Union Institute & University, 440 East McMillan Street, Cincinnati, OH 45206, USA. [7]National Museum of the American Indian, Smithsonian Institution, Washington, DC 20013, USA. [8]Georgia Department of Natural Resources, Historic Preservation Division, 2610 GA Hwy 155, SW, Stockbridge, GA 30281, USA. [9]Department of Biology, Creighton University, 2500 California Plaza, Omaha, NE 68178, USA. [10]Georgia Southern University, Department of Geology and Geography, P.O Box 8149, Statesboro, GA 30460, USA. [11]Skidaway Institute of Oceanography, Ocean Science Circle, Savannah, GA 31411, USA. [12]Department of Anthropology at the University of Illinois at Urbana-Champaign, 607 S Mathews Ave, Urbana, IL 61801, USA.
*Corresponding author. Email: vdthom@uga.edu

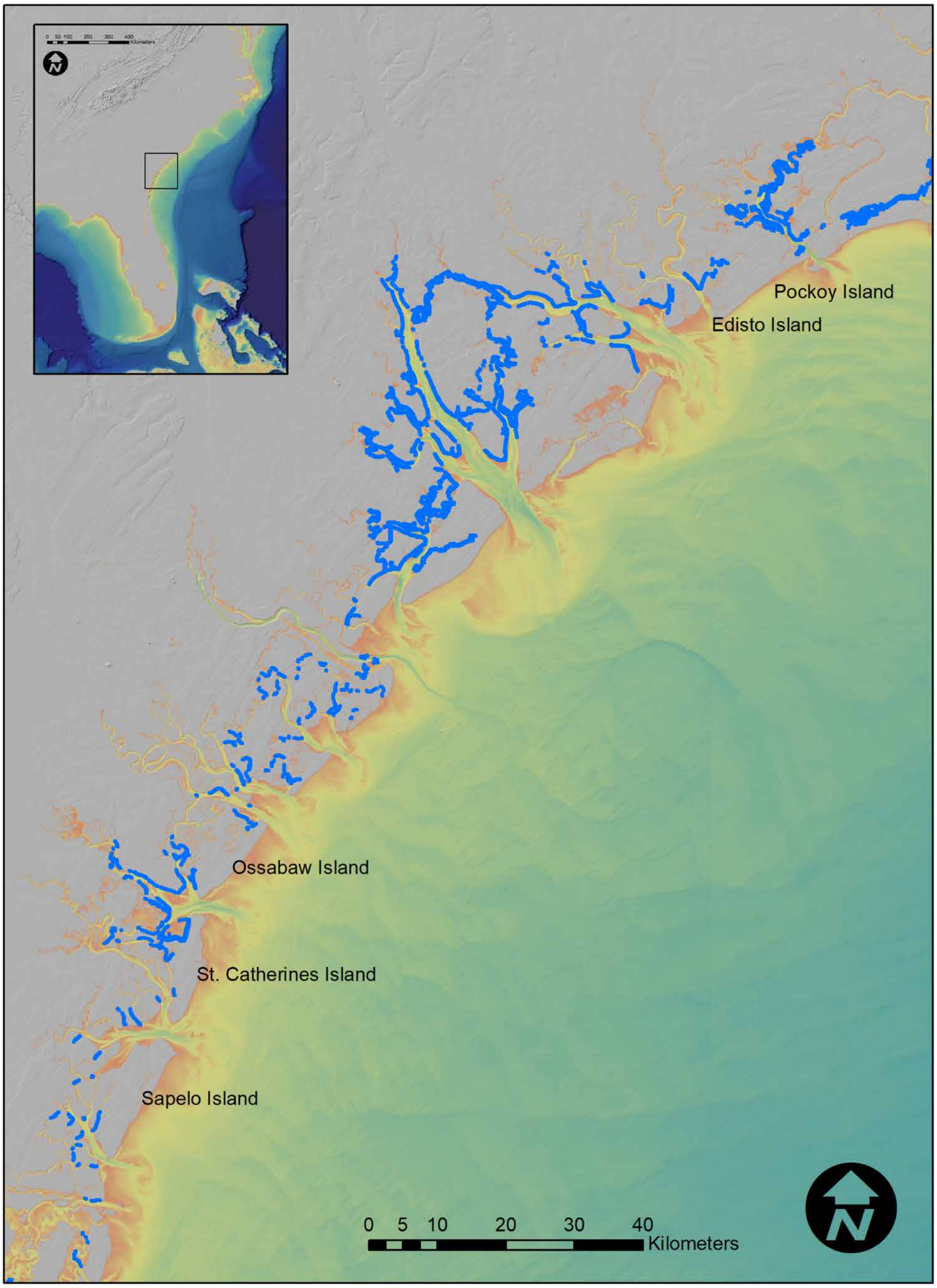

Fig. 1. The Georgia and South Carolina Coast showing islands that contain sites in the study area and the extent of mapped oyster beds in Georgia. Digitation of the oyster reef locations (in blue) was performed by M. Strickland for South Carolina and Clark Alexander's Laboratory for Georgia. All sites are located on barrier islands; however, exact locations are not provided to protect site locations from looting.

variation in the mean size of oysters. These results demonstrate that at a regional level, oyster fisheries were resilient and experienced multiple stable states over the last 5000 years before the 1900s. This is although the population grew exponentially from the Late Archaic to the Mississippian period and experienced shifts in political organization (e.g., from egalitarian to ranked systems) and changing economies (e.g., from foraging to a mixed economy that included some maize agriculture). Beginning in the 1900s, the oyster fishery experienced a marked collapse and has yet to return to its pre-1800 productivity (*10*). We believe that the archaeological evidence provides critical insights for ecosystem restoration by demonstrating where such fisheries are most resilient to long-term human influence.

The Native Americans who harvested oysters and other shellfish of the Georgia Bight were variously organized from small egalitarian villages to large stratified polities, yet all relied on estuaries and oysters in their economic pursuits (*11*). The earliest substantial occupation of the coast begins during the Late Archaic, followed by Native American occupation during the Woodland and Mississippian periods (detailed below). In middens found throughout these various periods, oyster was the most common invertebrate taxon regardless of the time period in linear sheet middens (i.e., refuse shell deposits) and midden-mounds, large mounded deposits of shell and other sediments. Perhaps, the most famous of the region's archaeological sites are its shell rings, massive circular ring formations of midden-mound deposits, some over 3- m tall. These shell rings, composed of oyster, other mollusks, vertebrate faunal remains, and artifacts, are thought to represent some of the earliest coastally adapted, pottery producing, egalitarian, sedentary villages in the United States (*12*, *13*). Around 3500 cal. BP, in some areas, there appears to have been a disruption in the fishery, and many sites were abandoned, possibly due to lowering sea levels (*14*). Despite the hiatus in shellfishing in some areas, people still resided along the coast, and when sea levels shifted again to favorable conditions, Native Americans reoccupied many of these areas, harvesting oysters and creating middens once again (*15*). While shell middens dating to the Woodland period (ca. 3100 to 1000 cal. BP) exist, few of these have appropriately collected samples similar to the other two time periods represented in our study and are thus not present in the current study. By around 1500 cal. BP, Native American groups increasingly focused on areas closer to estuaries and the coast in general (*15*).

By the Mississippian period (ca. 1000 to 500 cal. BP), the Georgia Bight saw exponential growth in population, possibly due to in-migration from other regions, the establishment of a regional settlement system, and eventually, the adoption of maize agriculture (*16*). During this time, the Guale (the 16th century historically known people of the northern Georgia Coast) were organized into expansive multitown polities with ranked systems of inherited asymmetry in leadership and social prestige (*16*). This likely played out as social status ascribed at birth determined by the genealogical distance from a single noble ancestor. Thus, the egalitarian social network of the Late Archaic (with leadership lacking inherited authority) shifted to one that was characterized by increased competition between groups. The resulting status competition with other groups led to proprietorship over key resource areas, including oyster reefs. With more people to feed, nearby shellfish beds inevitably experienced more substantial harvesting pressures, forcing increased reliance on harvesting eastern oysters from more distant intertidal habitats and/or substrates. At many of these sites, archaeologists have documented hundreds of individual household midden mounds typically dominated by oysters. At some sites, up to 600 midden mounds have been recognized. On the basis of studies of extant midden mounds, many of these would have been a meter high and 10 m in diameter before being reduced in height by historic agriculturally practices (*17*, *18*). Thus, the harvesting of oysters, even in the context of a limited degree of maize agriculture, still contributed to the overall Mississippian diet. Isotopic analysis of oysters and clams from both Late Archaic and Mississippian period sites from the Georgia Coast suggests that Native peoples harvested these resources throughout the year with a preference for oysters during the cooler months (*12*, *19*).

Isotopic studies of Late Archaic and Mississippian period oysters from the Georgia Coast indicate that Native American groups used a wide range of oyster reef habitats (*19*, *20*), based on the understanding that d18O water trends covary with salinity and that the absolute values reflect the range of habitat (*20*). These results suggest that the foraging areas for oysters were quite large; given the nature of canoe technology and knowledge of the twice-daily high-amplitude tides (ca. 3 m) for the Georgia Bight, distant beds could be traveled to daily, and a foraging radius of 10 km or possibly larger would not have been out of the question (*20*).

During the early 16th century, Spanish explorers, colonists, and Jesuit and Franciscan missionaries arrived on the Georgia and South Carolina coasts, significantly changing Native American lifeways (*21*). Indigenous population density plummeted, and villages sometimes congregated in mission towns, which were threatened by attacks and slave raids in the late 17th century. Spanish towns and missions contracted and were then abandoned (*22*). Although mission period populations continued to use oyster reefs, the resulting middens are more constricted across the landscape, mostly located near the mission towns (*16*, *23*). The intervening years saw the development of the plantation period with the legalization of slavery in Georgia in the 1750s (*24*). During the time that the plantations on the Georgia and South Carolina coast operated, oysters continued to be harvested; however, in much-reduced numbers compared to the time frames that Native Americans lived in these regions. This changed markedly in the early 1900s when the Georgia Coast became one of the leading producers of the world's canned oysters (*25*).

Given the trends that we describe above in shifts from the Late Archaic to the Mississippian period, we might expect that the size of the oysters harvested over time would diminish with increased harvesting pressures. In sum, there are several trends that suggest that this might be something that we would expect. First is the sheer nature of population growth and the number of people that would have needed to be fed during the Mississippian period versus the Late Archaic period sites. Second, given that we believe that there was greater territoriality among groups during the Mississippian period, then access to oyster reefs was likely more restrictive. Third, although there are some changes in subsistence, the timing of seasonal harvesting of oysters remained consistent over time. Thus, similar harvesting pressures, at least in terms of the timing of harvesting, existed for the Late Archaic and Mississippian periods. As a result of colonization and Native American depopulation, oyster reefs likely experienced fewer harvesting pressures during the period between the 1700s and late 1800s; however, during the late 1800s and early 1900s, these reefs were heavily harvested for canning and likely experienced greater pressure than ever before.

The results of our study of 37,805 eastern oysters from 15 Mississippian and Late Archaic sites from the South Carolina and Georgia coasts document both continuity and changes in size and their distributions along the coast over time. These trends, as we discuss below, do not conform to the expectations of reduced size of oysters during the time that Native Americans harvested oysters. The data do show that historic period exploitation resulted in significant reduction in live oyster reefs. This work highlights trends that can inform research regarding the stability of oyster reefs over time and how Native Americans communities along South Atlantic Coast may have contributed to the long-term stability of these oyster reefs.

RESULTS

Left valve height (LVH) and left valve length (LVL) increase in the archaeological oyster shell sample between the Late Archaic and Mississippian periods: mean LVH significantly increases from 72.9 to 75.6 mm, and mean LVL significantly increases from 38.2 to 41.4 mm (Table 1). Late Archaic and Mississippian samples are statistically different for both mean LVL [95% confidence interval (CI) = −3.43 to −2.93; $P < 0.001$] and mean LVH (95% CI = −3.28 to −2.09;

Table 1. LVL and LVH measurements (millimeters) for Late Archaic and Mississippian (Miss) sites.

Site	Island	Period	*N*	Min LVL	Max LVL	Mean LVL	Min LVH	Max LVH	Mean LVH
Pockoy Ring 1	Pockoy	Late Archaic	698	11.4	64.4	33.6	21.7	152.3	57.3
Spanish Mount	Edisto	Late Archaic	21,001	5.7	95.9	37.9	7.6	212.0	73.6
Cane Patch	Ossabaw	Late Archaic	2228	111.4	87.6	40.1	17.3	182.2	62.6
Ossabaw Shell Ring	Ossabaw	Late Archaic	1432	2.7	74.9	37.8	6.8	184.6	85.5
St. Cath. Shell Ring	St. Catherines	Late Archaic	557	18.4	75.3	44.3	25.0	148.4	72.2
McQueen Shell Ring	St. Catherines	Late Archaic	2021	19.9	84.8	43.7	34.9	171.3	73.9
A Busch Krick	Near Sapelo	Late Archaic	48	20.5	70.8	43.3	54.5	178.0	90.9
Sapelo Shell Ring 1	Sapelo	Late Archaic	65	18.3	81.7	35.3	38.1	123.6	65.3
Sapelo Shell Ring 2	Sapelo	Late Archaic	1057	14.3	74.9	34.1	25.7	202.9	65.3
Sapelo Shell Ring 3	Sapelo	Late Archaic	1008	5.2	65.4	32.1	28.8	150.7	58.4
Total	**Total**	**Late Archaic**	**30,115**	**2.72**	**95.8**	**38.2**	**6.8**	**212.0**	**72.9**
Finley's Pond	Ossabaw	Miss	1830	4.2	72.8	35.1	6.4	162.4	66.8
Bluff Field	Ossabaw	Miss	478	14.6	73.6	41.2	35.7	132.4	65.8
Meeting House	St. Catherines	Miss	5095	9.8	78.6	43.2	27.6	187.0	78.6
Kenan Field	Sapelo	Miss	237	18.4	70.9	42.3	33.3	132.1	71.2
Sapelo South	Sapelo	Miss	50	25.7	52.1	35.1	45.2	114.4	71.9
Total	**Total**	**Miss**	**7690**	**4.2**	**78.6**	**41.1**	**6.5**	**187.0**	**75.6**

$P < 0.001$). In general, this pattern holds when comparing oyster size between Late Archaic and Mississippian sites within the same foraging radius. Mississippian sites have statistically larger oyster shells than Late Archaic sites in the same foraging radii on both St. Catherines Island (LVH: 95% CI = −7.3 to −5.2, $P < 0.001$; LVL: 95% CI = 0.1 to 1.0, $P = 0.01$) and Sapelo Island (LVH: 95% CI = −8.9 to 1.9, $P < 0.01$; LVL: 95% CI = −9.1 to −6.6, $P < 0.001$). Ossabaw Island is of exception as it witnessed a statistically significant decrease in oyster size across time (LVH: 95% CI = 16.5 to 20.8, $P < 0.05$; LVL: 95% CI = 2.0 to 3.5, $P < 0.05$). Oyster size also varies between levels within single sites. At McQueen Shell Ring (LVH: $X^2 = 76.1$, $P < 0.001$; LVL: $X^2 = 58.1$, $P < 0.001$), St. Catherines Shell Ring (LVH: $X^2 = 30.4$, $P < 0.001$; LVL: $X^2 = 22.4$, $P = 0.004$), and Sapelo Shell Ring 3 (LVH: $X^2 = 90.9$, $P < 0.001$; LVL: $X^2 = 76.7$, $P < 0.001$), there is a small yet statistically significant temporal decrease in oyster shell size through time during the Late Archaic Period (Figs. 2 and 3 and tables S5 to S8).

Oyster size also varies latitudinally, as indicated by a nonrandom pattern moving north to south, often clustering by island (Fig. 4 and Table 1). Tests for equality of variance find a significant difference among the variances of LVL and LVH for each site (LVL, $P < 0.001$; LVH, $P < 0.001$). At the mean level, sites are significantly different in regard to both LVH and LVL (LVH: $X^2 = 2092$, $P < 0.001$; LVL: $X^2 = 3057.9$, $P < 0.001$). A post hoc Mann-Whitney *U* test, however, shows that many but not all sites are distinguishable regarding these measurements. Much of the difference in oyster size variation is between islands. A geographical comparison of oyster size shows that sites grouped by island are significantly different regarding mean LVH and LVL (LVH: $X^2 = 2120$, $P < 0.05$; LVL: $X^2 = 782$, $P < 0.05$) (fig. S1), and a post hoc pairwise Mann-Whitney *U* test indicates that all islands are distinguishable, except for LVL between Edisto and Ossabaw islands ($P < 0.05$) (table S4).

The mean oyster length (LVH) was compared to the total length of oyster beds as mapped in 1889 and 1890 within a foraging radius of both 5 and 10 km from each site. We assume that oyster bed length correlates with density, productivity, and abundance of past oysters. A Spearman's correlation test shows a moderate and statistically significant correlation between LVH measurements and total oyster bed lengths in both 5 and 10 km foraging radii (5 km: $R = 0.58$, $P = 0.04$; 10 km: $R = 0.62$, $P = 0.03$) (Fig. 5 and table S3).

DISCUSSION

Late Archaic and Mississippian period oyster measurements correlate with the size of oyster reef habitat as mapped in 1889 and 1890 within site foraging radii (*26*), suggesting long-term stability in estuarine and marine habitats despite variable human harvesting practices. In addition, oyster size measurements at individual sites demonstrate that some oyster populations experienced harvesting pressure at the outset of human occupation during the Late Archaic. In the southern part of Ossabaw Island, the mean oyster size decreases for several periods (*6*). Overall, however, our data show growth in oyster size

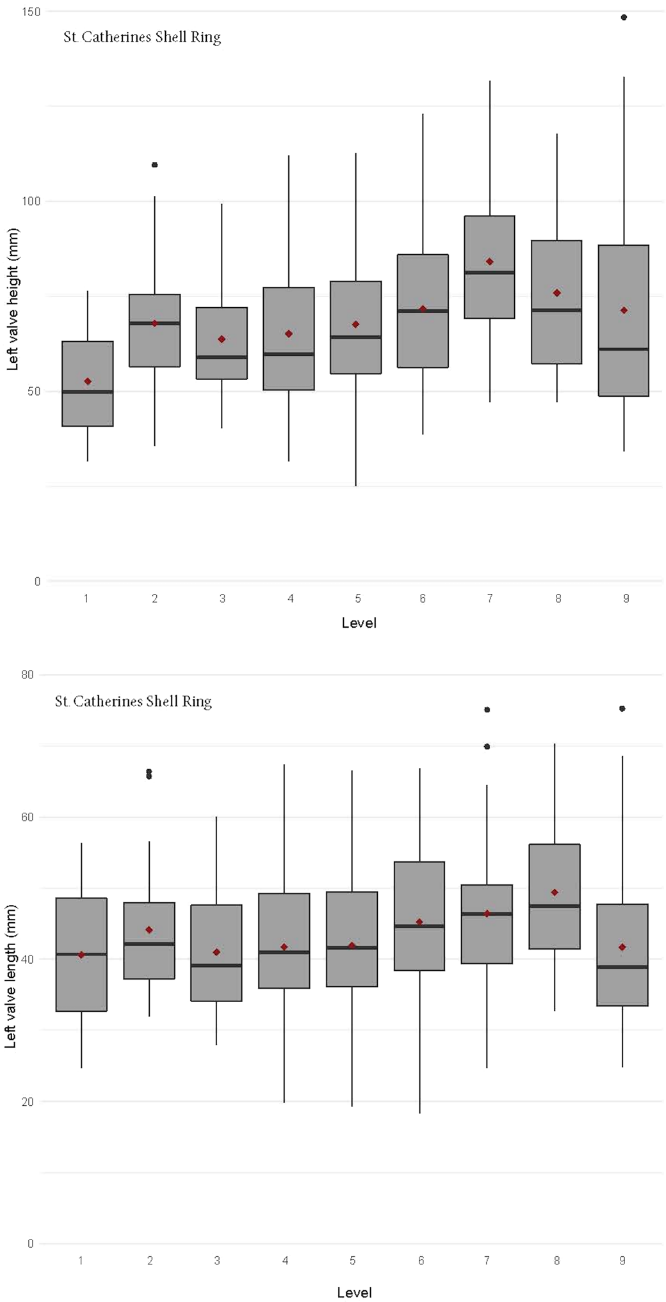

Fig. 2. Box plots showing variations in LVH and LVL measurements between different levels at St. Catherines Shell Ring. LVH measurements, top; LVL measurements, bottom.

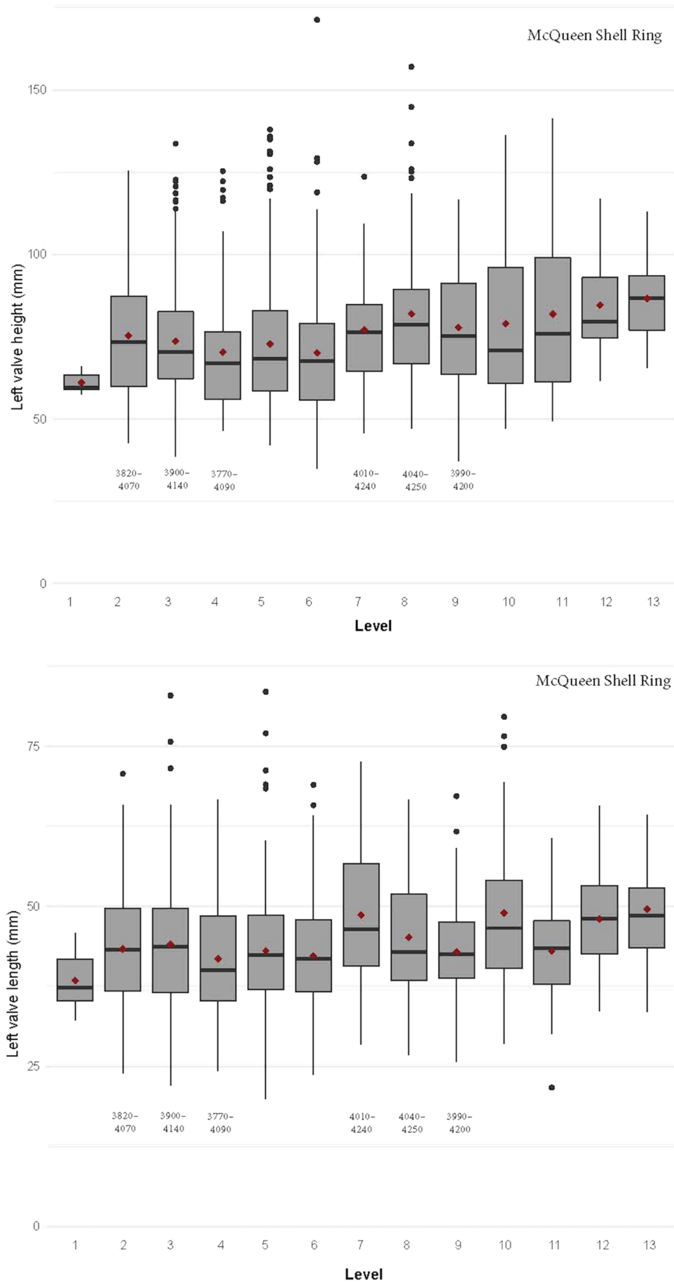

Fig. 3. Box plots showing variations in LVH and LVL measurements between different levels at McQueen Shell Ring. LVH measurements, top; LVL measurements, bottom. Radiocarbon dates are shown below box plots.

through time, implying localized increases in ecosystem productivity, either through human management practices or environmental change.

How do we account for this long-term stability? On the basis of our results, we suggest that when Native Americans used oyster reef ecosystems that there existed some kind of territoriality in fishing rights. Mississippian populations likely maintained considerable hierarchical control over oyster reef harvesting, and these territorial practices might have begun much earlier, perhaps parallel to ethnographic and archaeological evidence from fisher-hunter-gatherers elsewhere in the world (*27*). Along the Northwestern coast of North America, for instance, long-term "property" rights likely endured and were linked intimately with social institutions revolving around kinship and affiliation (*28*). Although technologies and environments probably shifted through time, Reitz (*29*) found considerable continuity in the kinds of estuarine fishes captured by Native Americans in Georgia from the Late Archaic through the Mississippian period, consistent with the findings reported here.

Overall, these data suggest that fishing/shellfish harvesting territories and governing practices may have had considerable antiquity. Larger regional systems of fisheries management could have functioned as ways to overcome collective action problems at both local and regional scales. Reitz (*29*) argues that common pool management

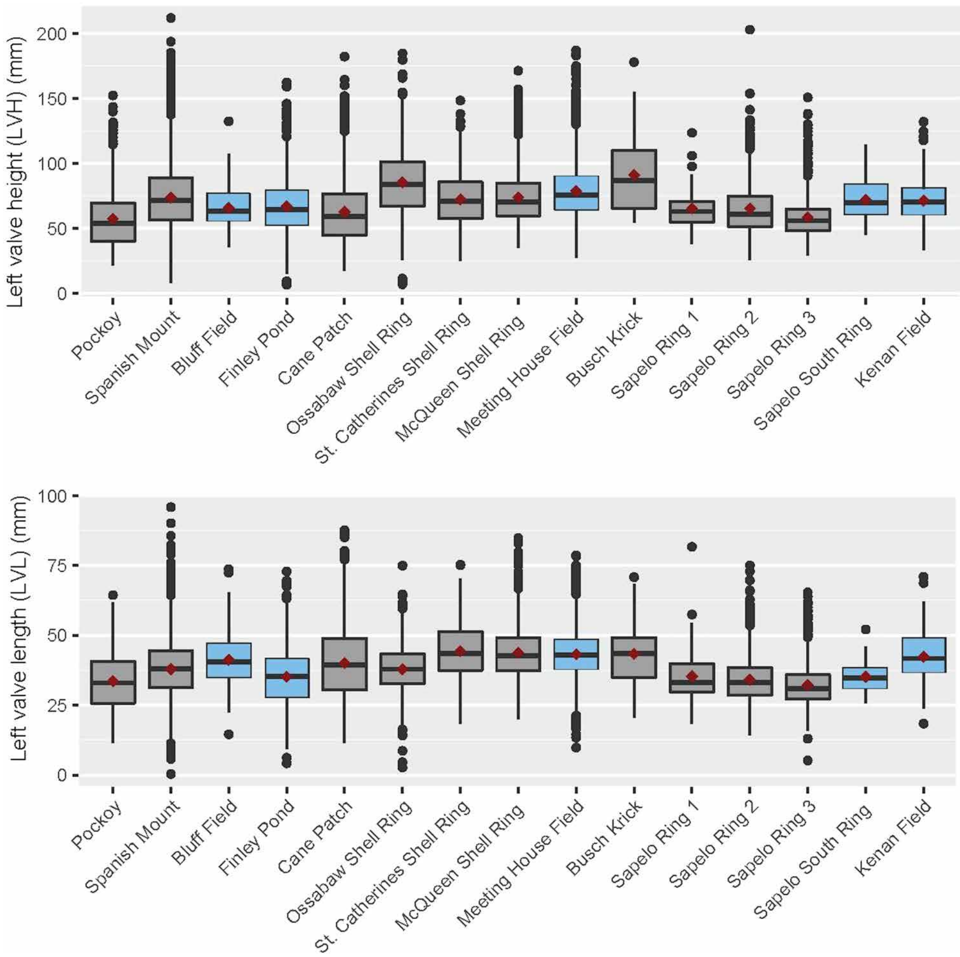

Fig. 4. Box plots showing a non-random pattern of variations in mean LVH and LVL between sites moving north to south. Mean LVH, top; mean LVL, bottom. Gray boxes are Late Archaic period sites, and blue boxes are Mississippian period sites. Sites are organized from north to south starting at the left.

might have governed where fishing and shellfish collection could take place and by whom, mitigating resource depression problems at both local and regional scales. Her study of fishes found that Native Americans and subsequently Euroamericans continued to harvest core species in the region from 2400 B.C. until the 16th century and, in some cases, at postcolonial sites harvesting persisted into the 19th century. In general, Native Americans captured fishes using mass capture technologies (e.g., nets and weirs). Despite intensive harvesting of these fishes, for the most part, such practices were sustainable over long periods, indicating to Reitz (*29*) that some form of social control and management of resources occurred along the coast. Adaptive controls, such as common pool management and proprietorship over beds, likely emerged with the onset of village formation along the coast as populations moved into productive new areas where resources could be procured (*29*, *30*). Villages were dependent, to a large extent, on local resources, therefore, and likely enacted practices to encourage the health and productivity of nearby reefs (e.g., perhaps seeding them with old oyster shells). Precisely what these practices were that promoted sustainability in oyster reefs is difficult to discern at this point; however, the patterns identified here point to such practices. In addition, each site and subregion experienced unique local histories, and these interactions reflect an overarching "complex adaptive system" that may have emerged early on in the region's history. While such practices were likely concerned overall with local-level resources, they would have nonetheless contributed to larger regional sustainability. Thus, this common pool management system likely had lasting effects on the oyster reef community. In the interim 200 years from the reduction in Native American populations to the rise of the market economy in the 1800s and 1900s, there is considerable continuity in oyster productivity. This suggests that Native American management of these resources has lasting legacy effects on the ecosystem, not unlike those observed elsewhere in the American South (*31*).

Beyond suggesting some mechanisms of Native American resource management, this research also has implications for modern oyster conservation and management. The Georgia Bight ecosystem evolved in concert with human use of estuarine and terrestrial resources over 5000 years—underscoring the fallacy of any purportedly "pristine environment" inhabited by "people without history" (*29*). Instead, the archaeological and paleoecological findings suggest a highly resilient pattern of harvesting practices and possible reef management of oyster use over this time frame. Such a perspective would not have been possible without the data provided by the archaeological samples from shell middens in the region. Furthermore,

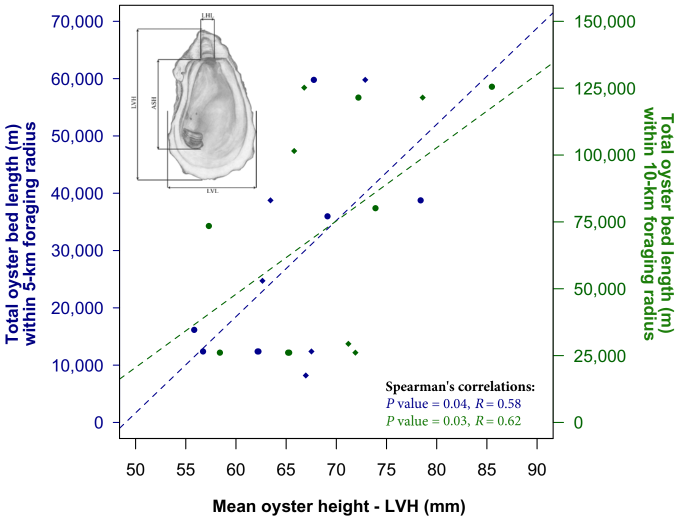

Fig. 5. Plot showing correlation between mean LVH and total oyster bed lengths within 5 km (blue) and 10 km (green) foraging radii. Diamonds represent Mississippian period sites and circles represent Late Archaic period sites. Inset oyster drawing shows measurement locations on *C. virginica* [adapted from (*5*,*6*)]. Drawing by E. R. Parham. ASH, anterior scar height; LHL, left hinge length.

these data indicate that large-scale harvesting of oysters from the region can be sustained with proper institutions in place to protect against overexploitation. With the emergence of market-based exploitation in the late 1800s and 1900s, millions of pounds of oysters were harvested from the Georgia Bight (*25*, *32*), resulting in an overall ~86% decline in the areal extent of oyster reef habitat as measured by the 1889 survey (*10*, *17*, *26*). By 1974 to 1977, many of the beds documented in 1889 survey no longer support living reefs, and with the demise of industrialized harvesting, only a few thousand pounds were being collected per year (*26*, *32*). Only 8% of live oyster beds documented in 1889 were live oyster beds in 2018 (*33*). Beyond overexploitation, the loss of freshwater input has affected the salinity along parts of the coast and may be partially responsible for the shifts in some beds (*32*).

New legislation and costly conservation programs today encourage the restoration of oyster reef farming on the Georgia Bight (*34*). We argue that the paleobiological record from archaeological sites in the region can help managers make informed decisions about such ecosystem restoration, using 5000 years of oyster reef history to pinpoint places where oyster farming may be more efficiently practiced. This, of course, is more complicated than merely looking at the data in the present study and must be coupled with current localized environmental data to provide a comprehensive picture of oyster restoration. Nevertheless, the long-term history of oyster productivity demonstrates that not all parts of the Georgia Bight have equal potential as oyster habitat, particularly with regard to the mean size of individuals harvested, to say nothing of the dependent estuaries. In coastal California, long-term archaeological datasets of red and black abalones (*Haliotis rufescens* and *Haliotis cracherodii)* have helped identify important past nursery sites and highlight places for habitat restoration (*35*, *36*). In the Pacific Northwest, similar archaeological research on Native American clam gardens and clam management systems demonstrates the relevance of past human subsistence, land use, and management practices for informing modern nearshore ecological productivity (*37*). Our work in coastal Georgia further demonstrates how deep historical data can provide concrete metrics for restoration, including site selection, past environmental productivity, and suitability for sustained human harvest. The next step will be to incorporate these data along with information on modern ecosystem services in discussions between scientists, resource managers, local stakeholders, and the descendent communities whose ancestral lands are the Georgia and South Carolina coasts.

Shellfishing has been a critical human subsistence strategy around the world for thousands of years (*38*). This was never a matter of merely picking up mollusks for food but a practice governed by a diversity of social rules that operated at the community, individual, and regional levels. Then and now, human survival is governed by complex behaviors regarding key subsistence resources. Kirby (*25*) underscores the importance of documenting historical sequences of expanding and collapsing oyster fisheries to define which parts of the coast are in the greatest danger. The long-term histories buried in shell middens on the Georgia Bight may hold a key to its future, provided we factor in the social and environmental forces that have affected oyster and human populations alike.

MATERIALS AND METHODS

A total of 37,805 eastern oysters (*C. virginica*) were measured from 15 Late Archaic and Mississippian period sites situated along the South Atlantic Coast (Fig. 2). LVL and LVH measurements (millimeters) were taken following a standard method outlined by Lulewicz *et al.* (*6*). Although LVH is more commonly used in oyster paleobiology studies, we also include LVL measurements because it too is an important proxy for paleoenvironment and human population pressures (*5*). All data analyses were conducted using the statistical software R (*39*). A Bartlett and Shapiro-Wilk test were first used to examine homogeneity of variance and normality of the data, respectively. Since the data are not normally distributed or homoscedastic, a nonparametric Kruskal-Wallis test was used to compare mean LVH and LVL between sites, and a post hoc pairwise Mann-Whitney *U* test was used to examine which sites are distinguishable in regard to mean LVL and LVH. To reduce the possibility of type I errors associated with multiple comparisons, a Holm correction was added to all Mann-Whitney *U* tests. Emphasis was placed on differences between islands and between Late Archaic and Mississippian period sites within the same 5- and 10-km foraging radius. A Kruskal-Wallis test and a Mann-Whitney *U* test were also used to compare oyster size between different levels at McQueen Shell Ring, Sapelo Shell Ring 3, St. Catherines Shell Ring, and Ossabaw Shell Ring and between sites clustered on Edisto Island, Ossabaw Island, St. Catherines Island, and Sapelo Island. A Student's *t* test was used to compare mean LVH and LVL between all Late Archaic and Mississippian sites. Differences were considered statistically significant when $P \leq 0.05$. A Spearman's rank correlation test was used to examine the strength of the relationship between LVH and total oyster bed lengths (meters) in 5- and 10-km foraging radii of 10 sites. Two Late Archaic sites (Spanish Mount and Cane Patch) were excluded from the correlation analysis, as these sites appear to be mounds, as opposed to rings, and thus likely aggregation sites rather than habitation sites. Data on oyster bed length were collected from oyster bed maps made in an 1889 survey of Georgia (*10*, *33*) and from 1890 in South Carolina (*40*). These were then georeferenced and digitized in ArcGIS by Alexander's Laboratory and M. Strickland, respectively, for the current analysis.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/28/eaba9652/DC1

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