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Shellfishing, sea levels, and the earliest Native American villages (5000–3800 yrs. BP) of the South Atlantic Coast of the U.S

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Shell ring archaeological sites are one of the most visible site types along the lower South Atlantic Coast of the United States. These cultural sites are large, circular to arcuate piles of mollusk shells with some reaching over three meters in elevation and over 100 m in diameter. They are comprised largely of mollusk shells (e.g., Eastern oyster, *Crassostrea virginica*), but also contain early pottery, nonhuman faunal remains, and other artifacts. Our work establishes that they represent the earliest widespread Native American villages occupied year-round in the Eastern Woodlands of North America. Significantly, our results from sea-level modelling and isotope geochemistry on mollusks establish that the inhabitants of these earliest villages (ca. 5000–3800 yrs. BP) lived within a fluctuating coastal environment, harvested certain resources year-round, and targeted diverse habitats across the estuaries. Both the growth and decline of these earliest villages are associated with a concomitant rise and lowering of sea level that impacted the productivity of the oyster reef fishery along the South Atlantic Coast. Despite these large-scale environmental changes, this research indicates that Native American fishing villages persisted along the coast for over 1000 years.

Keywords Ecosystem evolution, Native American, Isotope Geochemistry

The move for human communities to settle into the landscape and reduce their overall mobility is a transition that took place at various times in history among disparate geographic communities[1,2]. Historically, researchers portrayed such initial shifts towards sedentism and ultimately village life often as "push" or "pull" relationships with environmental circumstances[3]. More recently, such research adopts a more complex view of the emergence of sedentary communities and village life that includes a greater consideration of both the social and environmental factors that were also historically contingent aspects of the transition to village life[4,5]. However, large scale studies that address the conditions under which village life emerged and ultimately persisted tend to be site focused with few regional studies conducted rooted in large scale comparable datasets. Such large-scale perspectives are important to understand complex relationships that human communities have with their environments. The reality of such socio-ecological systems is complicated, frequently resulting in messy datasets that often do not demonstrate the clear correlations that researchers search for in the archaeological record[6].

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Here, we present results that demonstrate the complicated relationship between the earliest village communities of the South Atlantic Coast of what is now the United States and the dynamic coastal environment within which they dwelt for over 1000 years. Global research regards both the transition to village life and adaptation to coastal environments as two of the key transitions in human history[7,8]. The earliest villages in the region present an ideal case study by which to explore how both human institutions and human practices articulated with large and smaller-amplitude environmental shifts. These relationships provide insight into how researchers should study and understand early coastal villages.

The earliest villages in eastern North America are large, circular to arcuate shell rings consisting of piles of mollusk shells (e.g., Eastern oyster, *Crassostrea virginica*), pottery, nonhuman faunal remains, and other artifacts[9] (Fig. 1) (see SI for a detailed discussion). Our recent research demonstrated that, far from islands all being occupied in the same general time frame, shell-ring villagers frequently abandoned islands only to return to them later[9]. Our high-resolution dating program now allows us to order these shell-ring villages in sequential time[9]. Our past work regarding the isotope geochemistry at a few of these sites show that collection of mollusks occurred throughout the year[10] frequently with opposing seasons in the same deposit, suggesting at least some portion of the population resided at any given shell ring site year-round. These data coupled with other studies of season of occupation, the density and distribution of pottery discard, and site structure all point to the idea that these sites represent early villages with a circular habitation zone and centralized plaza that was kept free of dense shell deposits[10–14]. Shell deposits likely accumulated around and beside houses and as they shifted over time a ring-shaped midden developed as the result of both domestic and ceremonial feasting[12,14–16]. The current study presented here was implemented to see if the patterns of season of collection of oysters and clams at the few sites where we had intensively sampled mollusks for isotope geochemistry would be replicated across the region and therefore we could make broader statements about how these settlements experienced environmental shifts. Prior studies indicate that the decline in the creation of shell rings coincided with the lowering of sea levels and local environmental change[17–19]; however, the exact processes and implications of this shift in settlement and its connection to sea-level change remain less well understood, and how these villages persisted for centuries in the region remains understudied. Specifically, we present the results of our isotope geochemistry project, the largest of its kind on archaeological mollusks. The patterns observed for all the sites in our sample are consistent and replicate patterns of earlier studies where the isotope geochemistry and other datasets indicate year-round settled occupation—or villages. While it would both be cost and time prohibitive to replicate the complementary research (e.g., large scale excavations) and the detailed studies for each of these sites, we argue that the isotope geochemistry alone provides a sufficient proxy by which to infer patterns at the regional level for these cultural sites. Following this logic, our results demonstrate that the earliest villages emerged within a fluctuating environment, harvested resources year-round, and targeted diverse habitats across the estuaries. Both the growth and decline of these earliest villages are associated with a concomitant rise and lowering of sea level; however, despite a major impact on oyster reef fisheries, communities persisted along the coast.

Results

Sea-level modeling and oyster reef availability

Sea level along the Georgia and South Carolina coasts at ca. 5000 Before Present (BP), the age of the earliest shell rings in the region, would have been substantially lower than present-day mean sea level (MSL)—likely between 1.5 and 4.5 m below present MSL, as reconstructed by multiple proxies in several studies[20–24]. In order to understand the viability of marine resources under these coastal conditions, we developed a spatial model for estimating intertidal zones under three different sea-level scenarios (1.5 m, 3 m, and 4 m below present), reflecting possible conditions at 5000 BP. Our model is based on a simple bathtub-style approach (i.e., we do not account for changes in local coastal geomorphology, though we do account for localized conditions of MSL based on multi-proxy studies, as discussed above, and local tidal variation along the Atlantic Coast as measured by tidal averages at NOAA water-level stations). Our results show a drastically different structure of coastal ecosystems than conditions of today (Table 1). Many of the historically mapped shellfish habitats of the recent

Fig. 1. Aerial photograph of Fig Island Ring II off the coast of South Carolina, which currently is being inundated by sea-level rise (Photo and permission under CC BY by A. J. Koelker, Principal, Koelker & Associates, LLC).

SEA-Level scenario	Viable oyster beds	Potentially viable oyster beds	unviable oyster beds
GMSL	1844	1375	278
GMSL—1.5 M	1104	687	1706
GMSL—3.0 M	432	411	2654
GMSL—4.0 M	278	277	2942

Table 1. Total length (m) of oyster reef beds under different sea-level scenarios (oyster bed lengths were collected from oyster bed maps made in an 1889 survey of Georgia [Drake 1891] and from 1890 in South Carolina [Burrell 2009]).

past[25,26], largely located in intertidal zones between the Silver Bluff and Princess Anne Ancient Coastline Deposits (ACDs), may have been in supratidal zones and, as such, unviable for shellfish under these lower sea-level conditions. However, even in a 4 m below present scenario, several hundred of these known oyster beds would have been located in intertidal zones and were therefore likely available for exploitation by residents of the Southeast Coast. Future work on reconstructing salinity gradients can help explain the relationship between location relative to the ancient shoreline and estimated salinity of harvested shellfish.

Season of harvest data

Mollusk shell oxygen isotope composition ($\delta^{18}O_{carbonate}$) is a product of the oxygen isotope composition of water ($\delta^{18}O_{water}$) and water temperature at the time the shell was precipitated[27,28]. $\delta^{18}O_{water}$ covaries with salinity according to mixing of fresh and marine waters in a habitat[29,30]. For this reason, incremental $\delta^{18}O$ analysis of mollusk shells can be used to reconstruct site occupational histories based on season of capture archived in the shell matrix[31–34]. In this study, $\delta^{18}O_{carbonate}$ varied among all mollusk shells and within each site, with mean $\delta^{18}O_{carbonate}$ of − 0.4‰, ranging between − 5.6‰ and 4.0‰ for all shells. Most shells in the sample show a general sinusoidal $\delta^{18}O_{carbonate}$ profile, indicating seasonal fluctuations in water temperature and allowing us to determine season of capture based on the $\delta^{18}O$ value at the growing edge at time of capture. Our results show that, for all sites, shells were harvested year-round, with multiple seasons represented. However, the majority of shells were harvested in winter. More specifically, 48% of shells ($n = 112$) were harvested during winter, 24% ($n = 55$) in the summer, Spring is 7% (n = 16) and Fall is 10% (n = 23); 12% of shells ($n = 27$) did not have enough variation in their $\delta^{18}O_{carbonate}$ profiles to determine season of capture (Fig. 2). Clams showed a wider variation in season of capture, with more shells harvested in summer (32%) compared to oysters (12% harvested in summer).

Habitat harvest profiles and temporal isotopic trends

The sinusoidal $\delta^{18}O_{carbonate}$ profiles also allow us to constrain summer $\delta^{18}O$ values, as indicated by the most negative value within each shell profile, and to estimate $\delta^{18}O_{water}$ and salinity values for each shell, using a series of equations (see methods) based on a local salinity gradient and established relationships between $\delta^{18}O_{water}$ and salinity in the region[32,34,35]. Estimating salinity allows for a reconstruction of habitats used and, consequently, shellfish harvesting practices. However, it should be emphasized that these estimates are subject to uncertainty due to multiple factors. Space limits our discussion of this uncertainty, but it has been described in detail elsewhere[34,35]. A summary of sources of uncertainty would include possible growth rate changes that affect sample time averaging of each $\delta^{18}O$ value, variation in the temperature at which shell growth ceases (assuming it stopped at all), inter and intra-annual variation in salinity and $\delta^{18}O_{water}$, changes in the local salinity/ $\delta^{18}O_{water}$

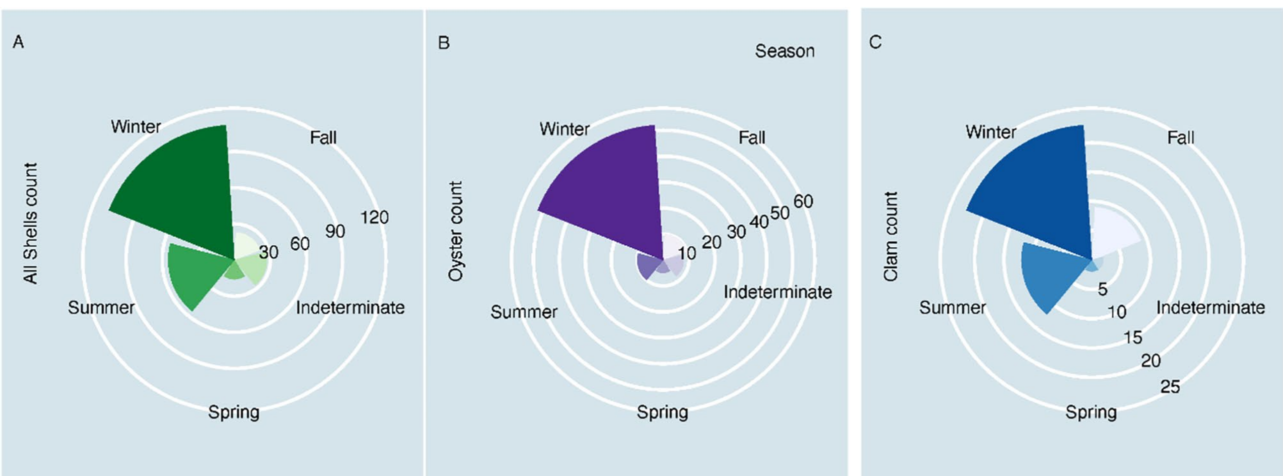

Fig. 2. Graphs showing seasonal trends in mollusk collection for (**A**) all shells in study, (**B**) just oysters, and (**C**) just clams.

relationship, and imprecision in both the $\delta^{18}O$ temperature equation and the salinity/ $\delta^{18}O_{water}$ slope. These will result in a salinity uncertainty of several psu that cannot be confidently quantified. Consequently, these salinity estimates should be viewed as qualitative, and interpretation should not hinge on single shells records or subtle differences in value, but rather should rely on statistical comparison between large sample sets as we have attempted here. If uncertainty in these estimates exceeded the environmental signal, then each site would likely yield similar psu ranges and values, but instead we see distinct changes between several sites.

Estimated $\delta^{18}O_{water}$ ranged between − 2.9‰ and 2.6‰ across all shells in the sample. Estimated salinity averaged 30 practical salinity units (psu) across all shells and within each site, ranging between 4 and 46 psu (Fig. 3A). This indicates that people were targeting a wide variety of habitats, ranging from oligohaline (freshwater) to euhaline (seawater). Most shells had estimated salinity values that fell within the salinity tolerance for each species, although outliers were not far outside of the expected range and are completely plausible considering the uncertainty in the related measurements.

In addition to measuring variation in salinity values to infer habitats utilized, we also integrated salinity data with recent radiocarbon models by Thompson and colleagues[9] to reconstruct salinity patterns across time, likely reflecting environmental and sea-level change. More specifically, Thompson and colleagues use Bayesian modeling of radiocarbon samples to date and order the timing of Late Archaic shell-ring and shell-mound sites along the South Carolina and Georgia coast, including sites in this study. Figure 3B shows the mean and range of salinity values for shells from each site arranged in chronological order. However, South Carolina is hydrologically unique compared to Georgia and may have experienced differential impacts of sea-level change on oyster reef viability (see Fig. SI2). For this reason, we separated sites by state in the figure. As shown in Fig. 3B, estimated salinity values from rings in South Carolina were high and persisted across time. However, for shell rings in Georgia, salinity values undulated across time, with the lowest salinity values in shells from the oldest (*Hokfv-Mocvse*) and youngest (Sapelo Ring III) shell-ring sites.

Discussion and conclusion

Our data indicate that there are a number of different traditions and institutions practiced by early villagers along the coast that facilitated their long-term resilience to fluctuating environmental conditions or what could otherwise be termed a sustainable socioecological system. Sustainability in this sense is the intermeshing of social and natural systems that allows for the long-term persistence of lifeways in a relatively recognizable pattern of core components[36,37]. This does not mean that the system is unchanging but rather is altered to maintain continuity in the face of both pulse and press environmental shifts[37]. In the case at hand, we make the following observation. First, although some South Carolina–coast villages tended to harvest from more restricted habitats, the overall pattern was for ring villagers to harvest from more diverse habitats regardless of time period. The collection of mollusks from different areas of the landscape was likely related to embedded traditions involving proprietorship of reefs[38], perhaps linked to kin-groups, sodalities, or other networks of users that may have "owned" or "controlled" or "monitored" access to specific harvesting areas. Furthermore, diverse harvesting could also help promote reef productivity and sustainability in the face of harvest pressures, especially within a shifting environment[30–32].

Prior to our study, only two Atlantic Coast shell-ring villages indicated year-round collection and, by extension, inhabitation by settled villagers (see our discussion in the SI). Our study now shows that this is the dominant pattern for these settlements and that few, if any, of these sites indicate that they were solely special-use locations by dispersed people. These data also indicate shell-fishing preferences of early villagers along the coast, with a focus on harvest during colder months of oysters (although with year-round collection) and, more regularly, year-round collection of clams. The focus for oyster harvesting during colder months, although not exclusive to them, could be related to the higher suitability to pathogenic diseases, fisheries management, or culinary preferences. It is evident that this pattern held across all the sites we sampled.

When we aggregate all the isotopic data by time, there is a distinctive fluctuating pattern regarding the overall salinity trends among the sites for the entire time period that villagers occupied shell rings. This suggested that, far from being a stable environment, the geochemistry of the estuaries experienced fluctuations during the time the rings were occupied. This is likely correlated with either more variable rainfall in the region and possible fluctuations in sea level, given that both have been argued for during this time frame[20,39].

Perhaps the clearest pattern in the aggregate isotopic data is that the lowest salinities are observed for the earliest and latest of the rings in the study. The earliest ring, *Hokfv-Mocvse* (Muskogean for "new seashell"), is the only pre-pottery shell ring in the sample, and it clearly shows not only year-round occupation but also a reliance on estuarine resources very early in the overall intersite sequence[40]. Prior to 5000 years BP, multiple sea-level studies in the region estimate levels well below modern sea levels, and several of these studies indicate 3 mbp (meters below present) levels or more[22,23,41–43]. Although researchers note the possibility that estuarine resources were present at this time, few settlements before the work at *Hokfv-Mocvse* indicated that Native peoples harvested these resources[44]. Our sea-level modeling using the location of historic oyster reefs demonstrates that even at 3 mbp, considerable reef resources, if located in the same general environments, would be available for early villagers to harvest. Furthermore, the relatively low average salinities of the oysters from *Hokfv-Mocvse* track with the lower predicted sea levels at this time, because more freshwater inputs into the estuarine system and increased distance to euhaline conditions would have resulted in a decrease in salinity regimes recorded in the estuarine resources in the immediate area of the site.

The very youngest ring displays similar lower overall salinities to those of the earliest and oldest known ring villages. In fact, the overall salinities of the oysters at this ring (Ring III of the Sapelo Shell Ring Complex) are even lower. Like *Hokfv-Mocvse,* the low overall salinities of Ring III correlate with a sea-level regression, given that multiple studies indicate a drop in sea level at this time, reaching 2.5 and 3.15 mbp by ca. 3800 and 3600 cal.

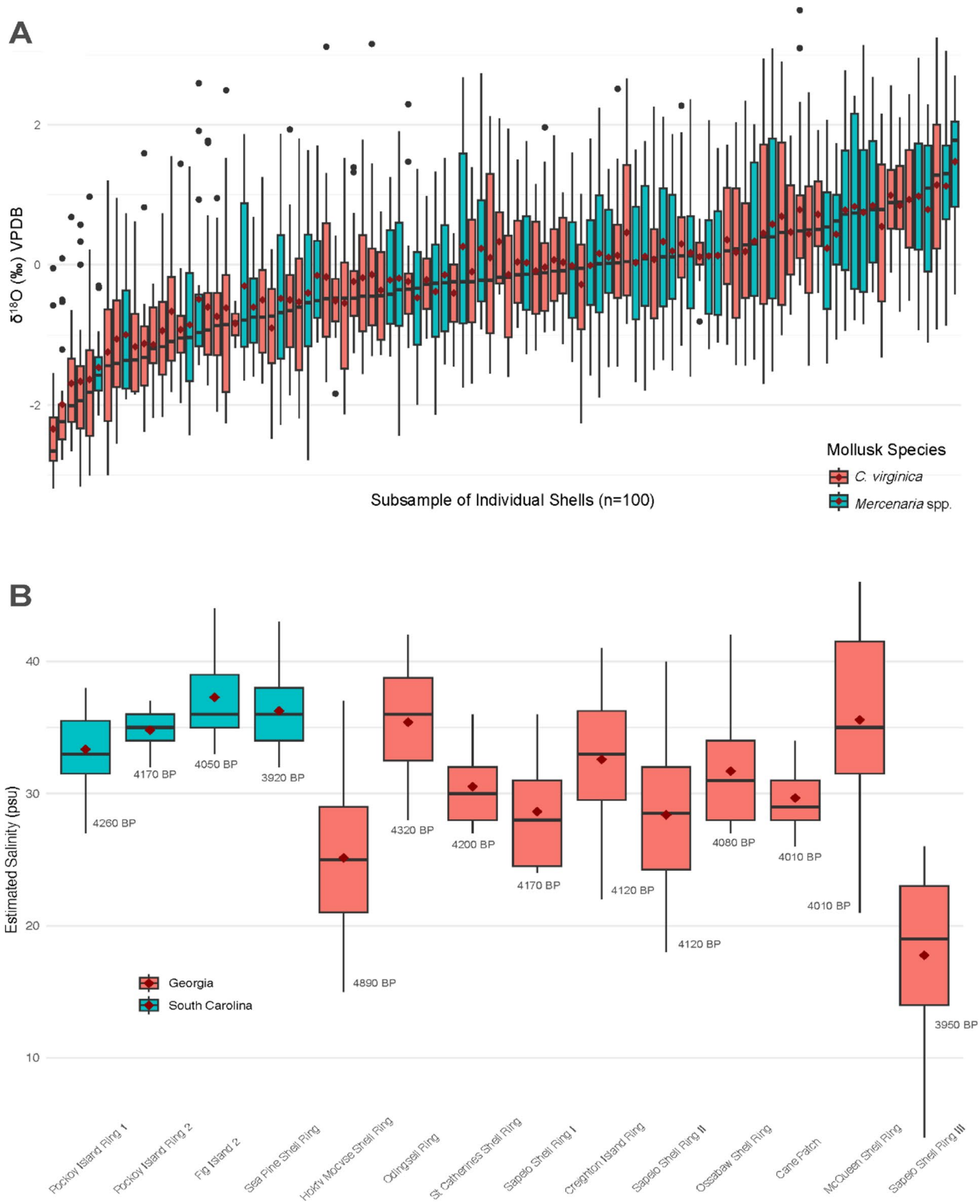

Fig. 3. (**A**) Box plots showing range of $\delta^{18}O$ values among a subset ($n = 100$) of individual shells included in study ordered by median. Red diamonds indicate the mean $\delta^{18}O$ value for each shell. (**B**) Box plots showing range of salinity values estimated from shell isotopic measurements by site, arranged by time and geographic location with the medium modelled date provided next to each box plot (South Carolina vs. Georgia) (see .

BP, respectively, possibly approaching a low of up to 4 mbp sometime before or at 2700 cal. BP[18,22,23,43]. For the northern half of the Georgia Coast and its immediate vicinity, the creation of shell-ring villages ceased. Although some shell-ring villages continued in South Carolina, these are only represented by a few sites and are among the smallest of the rings in this area compared to the South Carolina rings in our sample for this study.

The low salinities at the start and end of the phenomenon of shell-ring villages is likely related to sea-level change and climate shifts. For example, the major river systems (e.g., the Altamaha River) are the drivers for more freshwater in these areas during the lowstand. If we assume that such rivers had a similar discharge as today, then channels would have been more incised and would extend farther into the shelf, so wetlands/estuarine resources would be farther away from villages in these areas than they would be from ones situated within the smaller river systems. Consequently, fisheries and their attendant harvestable species would have shifted as well. We argue that this also holds true for the fluctuations that we see within the time frame that shell rings are occupied. Despite oscillations in climate and environment, it seems that shell-ring communities developed strategies of resilience that include diverse harvest practices and village relocation and reinhabitation[9]. Furthermore, although we do see an overall reduction in the number of archaeological sites after cal. 3800 BP, in the coastal zone, there were portions buffered against these shifting environmental conditions—most notably, in areas along the coastline where large rivers deposit sediment into the estuaries[19,44]. By cal. 3500 BP, very few shell rings existed, and these latest ones were only found far to the north along the South Carolina coast[9]. And although there certainly are large archaeological sites in the interim, large-scale villages that harvested shellfish would not appear again in any appreciable number until around a thousand years later. Despite this shift which we document in a number of publications[10,19,44] shell ring villages as an institution existed for over 1000 years, which certainly speaks to the resilience of these social formations.

The research presented here speaks to the complex relationship that humans have with their environment. In order to understand the conditions under which early villages emerged and persisted for centuries we need large scale datasets that speak to these issues. What is clear from this large study of early villages along the South Atlantic Coast was that Native American communities were able to develop practices that were sustainable within certain thresholds for over 1000 years. Our study not only underscores the kinds of data needed to understand such complex human relationships but also provides insight into how this process of settling down occurred in North America and its attendant challenges in crafting a sustainable way of life for the Indigenous people of the region.

Materials and methods

Shell ring archaeological sites are found throughout the lower South Atlantic Coast. Here, we focus on a subset of these sites (Figure SI1). Specifically, we evaluate the region as a whole by modeling shifts in the ecosystem over time due to sea level change as they directly relate to oyster bed availability. We further examine these shifts in the archaeological record by sampling oysters and clams for isotope geochemical analysis. We detail the methods for both of these analyses below and provide primary data for the isotopic analysis of all samples in this study.

Sea level modeling and oyster reef availability

In order to understand the spatial patterning of changing past sea levels and the potential viability of historically-known and mapped oyster reefs, we developed a simple spatial model to reconstruct intertidal zones under three different sea level scenarios (1.5, 3, and 4 m below present), reflecting possible conditions at 5,000 BP (see Figure SI2). Our model is based on the Continuously Updated Digital Elevation Model (CUDEM) program of the National Oceanic and Atmospheric Administration (NOAA). CUDEMs, available for the entirety of the study area along the coast of Georgia and South Carolina, are 1/9th arc-second (~ 3 m) resolution coastal topographic-bathymetric elevation models that facilitate detailed modeling of coastal inundation at regional scale[45]. These data are available as tiles and provide elevation measurements relative to the North American Vertical Datum of 1988 (NAVD88). We preprocessed the data by reprojecting and mosaicking rasters across the entire study area and converting elevation measurements from NAVD88 to measurements relative to Mean Sea Level (MSL) through the addition of an interpolated surface representing the difference between NAVD88 and MSL across the entire study area, derived from data from NOAA water level stations.

This adjusted raster served as the basis for two-part (change in MSL and projection in intertidal zones) reconstruction for each sea level scenario. First, the variation from modern sea level (i.e., 1.5, 3, or 4) was added to the MSL raster, representing a bathtub-style sea level reconstruction. Then, in order to nuance this simple sea level model by the reconstruction of potential past intertidal zones, we interpolated the differences between various tidal averages (MHHW, MHW, MLW, MLLW) and MSL based on measurements from NOAA water level stations across the entire study area, before reclassifying the resulting rasters according to inundated areas and adding them together. The intertidal zone analysis was also applied to present day MSL conditions. The result of this modeling is a reconstruction of potential intertidal zones, based on a projected past sea level and modern levels of tidal variation along the Georgia and South Carolina coasts. ArcPy code for this analysis, conducted in ArcGIS Pro, is available upon request.

Finally, these coastal reconstructions served as a basis for comparison to historically-observed and mapped oyster reefs through the Zonal Statistics tool. Our modeling assumes that oyster reefs located in supratidal zones are unviable, those in intertidal zones are viable, and those in subtidal zones are potentially viable. Analyzing the locations of oyster reefs relative to tidal zones in each sea level scenario was facilitated by the Zonal Statistics tool in ArcGIS Pro, allowing for the calculation of how many historically-observed and mapped oyster reefs would have been viable in each of the three scenarios and under present day conditions.

Our analysis does not remove DEM artifacts related to modern construction or landscape modification, nor does our analysis account for the many ways in which topobathymetric data along the dynamic coast of the Southeast would have changed due to ongoing and continuous processes of coastal erosion. Similarly, it is likely that past tidal variation along the coast would differ from trends observed today in unpredictable ways. As such, our modeling provides an estimate of prior coastal inundation rather than an empirically-derived projection. Moreover, our use of historically-known and mapped oyster reefs likely underestimates the availability of oyster resources in the past, as oyster reefs that are no longer known would have likely been exploited in the past.

Isotopes

We incrementally sampled 234 oysters and clam shells from 11 sites along the Georgia and South Carolina coasts for oxygen (δ^{18}O) isotope analysis, producing some 4172 individual δ^{18}O isotope samples. Oxygen isotope analysis (δ^{18}Ocarbonate) of mollusk shells is used to reconstruct paleoclimates and examine human-environmental interactions, such as shellfish harvesting practices and the occupational history of cultural sites (e.g., were the sites used seasonally or occupied year-round)[34,46,47]. Mollusk shell oxygen isotope values are controlled by water temperature and ambient water oxygen isotope composition. (δ^{18}Owater). Moreover, δ^{18}Owater covaries with salinity values; therefore, δ^{18}Ocarbonate values in shells are correlated with both the temperature and salinity values of water in which they live and grow[27–30]. Incremental δ^{18}Ocarbonate sampling of mollusk shells reveal seasonal fluctuations in water temperature, and the δ^{18}Ocarbonate at the growing edge of the shell, representing time at collection, can reveal the season in which the mollusk was harvested[31]. Moreover, since salinity values exist on a gradient decreasing the further way you get from the open ocean, estimated salinity values from mollusk shells can be used to examine the range of habitats used[31].

The isotopic methods used in the study are outlined in full detail in Garland et al.[32] and Andrus and Thompson[34] (see also a discussion in the SI). Briefly, we only selected left oyster valves with a complete chondrophore and clam shells with an intact edge, and shells with epibiont activity on their interior surfaces were excluded from analysis as they were likely dead upon collection. Oyster shells were bisected along the chondrophore and clams along their axis of maximum growth using a diamond blade saw. The bisected shells were then adhered to microscope slides using CrystalbondTM adhesive. Each shell was sampled following reverse ontogeny (starting at the ventral margin in clams and growing edge in oysters) using a Grizzly Benchtop micro-milling system. For oyster samples, we targeted the internal chalky calcitic areas of the hinges, avoiding the darker foliated calcite and aragonite regions closer to the hinge surface. Our sampling paths followed growth increments as seen in reflected light. Oyster samples were taken adjacent to each other at an average of 300–400 mm in width and to a depth of 300–400 mm. Clam samples were taken from the inner aragonite layers along the transected margin. Samples were taken sequentially starting at the ventral margin, and were milled to a depth of approximately 0.5-mm. Approximately, 12–20 samples were obtained from each oyster and 20 from each clam. This allowed us to capture approximately one to two years' worth of growth prior to collection.

The powered carbonate samples milled from each shell were weighed in tin capsules and placed into Exetainer® 12 ml borosilicate glass vials. All samples were analyzed for δ^{18}O and δ^{13}C at the University of Georgia's Center for Applied Isotope Analysis and using a Thermo Gas Bench coupled to a Delta V IRMS with a GC Pal auto-sampler. The weighed samples were first purged of the atmosphere with helium and acidified with phosphoric acid to convert solid carbonates to CO_2 gas. After which, the gas was released back into the helium carrier gas to the IRMS. The values for each sample are reported in parts per mil (‰) relative to the VPDB standard by correcting to multiple NBS-19 analyses (typically 14) per run. NBS-19 was also used to assess and correct for drift and sample size linearity if needed.

Oxygen isotope profiles were created for each individual shell. These profiles allow us to examine seasonal fluctuations in oxygen values as the shells were growing and to estimate season of harvest. The plotted profiles were divided into equal thirds (see Figure SI3). If the first sample, which represents time of collection, falls below the bottom line then the shell was collected in the summer, and if it falls above the top line then it was harvested in the summer. If the first value falls between the lines, then the shell was harvested in either the fall or spring depending on the direction of the trend. Salinity was estimated from shell δ^{18}O values following published methods established for the local environments around Sapelo Island. Equations 1 and 2 were first used to estimate δ^{18}Owater values for each clam and oyster, respectively. The estimated δ^{18}Owater values were then used to predict salinity for each shell from Sapelo Island and St Catherines Island using Eq. 3. Equation 4 was used to estimate salinity from all other sites on Ossabaw Island and to the north. All raw isotope and salinity data can be found in Supplemental Tables S1 and S2.

Equations:

E1—Summer δ^{18}Owater value in clams: Water temperature (°C) = 20—4.42(δ18Oargonite – x); whereas 31 °C is assumed to be the threshold of summer growth cessation for clams[31]; δ18Oargonite is the most negative value in each clam's profile; and x = δ^{18}Owater.

E2—Summer δ^{18}Owater value in clams: in oysters: Water temperature (°C) = 16.5—4.3(δ^{18}Ocalcite – x) + 0.14(δ^{18}Ocalcite – x)2; whereas 28 °C is assumed to be the threshold of summer growth cessation for oysters; δ^{18}Ocalcite is the most negative value in each oyster's profile, and x = δ^{18}Owater. Additionally, a 0.2‰ correction was applied to convert VPDB to VSMOW.

E3—Estimated salinity: δ^{18}Owater = 0.13(y)—3.4; whereas δ^{18}Owater is calculated by Eq. 1 or 2, and y = estimated salinity (psu)[32].

E4—Estimated salinity: y = 0.093(δ^{18}Owater) – 2.1; whereas δ^{18}Owater is calculated by Eq. 1 or 2, and y = estimated salinity (psu)[32].

Data availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. All raw data measurements are available through the Georgia Coastal Ecosystem Long Term Ecological Research Network website: https://gce-lter.marsci.uga.edu/. Additional data related to this paper may be requested from the authors. Researches needing access to any data in this paper should contact Victor Thompson at vdthom@uga.edu.

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Author contributions
V. D. T., M.S. K. S. conceived and designed the study. CJG, MH, VDT, MS, DHT, CFTA, CH, IHL contributed and analyzed data and interpreted results. VDT, CJG, MH coordinated and drafted the manuscript. VDT, CJG, MH, MS, KS, RC, EB, CA, DHT, IHL, CH, CFTA, AS edited and contributed to the manuscript.

Competing interests
The authors declare no competing interests.

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