**The Effects of Shellfish Harvesting by Aboriginal Inhabitants of Southwest Florida
(USA) on Productivity of the Eastern Oyster: Implications for Estuarine
Management and Restoration**

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ABSTRACT

Oyster reefs in Southwest Florida (USA) have been integral to estuarine ecology throughout the Holocene. Though *Crassostrea virginica* has never been commercially harvested, aboriginal people used the oyster substantially, accumulating middens between 5000 BC and AD 1700. A conservation paleobiological / historical ecological study of oysters from middens and modern reefs within Estero Bay (EB) and Pine Island Sound (PIS) determined if oyster productivity changed due to aboriginal overharvesting. Archaeological samples came from sites including the Late Archaic (LA, 2000-500 BC) of PIS and the Caloosahatchee (Cal, 500 BC-AD 1500) of EB and PIS. These samples were compared with natural oyster death assemblages from neighboring modern reefs. Methods comprised measuring oyster convex valve lengths and sectioning shells to count ligament pit growth lines that served as proxy for growth rate. The biologic taphonomic grade was also compared after scoring the interior valve surface; biologic grade is near pristine for oysters collected live for consumption. Archaeological samples exhibit significantly better taphonomic grades when compared to modern assemblages, confirming the hypothesis that oysters were harvested for food. Valve length decreased significantly from LA to Cal time, whereas modern assemblages were indistinguishable from LA collections. Because the Cal samples span 4 climatic intervals, the results suggest that climate change was not responsible for shifts in productivity. Results support the hypothesis of overharvesting during Cal times. They also suggest that modern oysters retain the capacity for growth, and indicate that aboriginal activity did not result in a permanent microevolutionary shift. The results are also relevant for the ongoing

discussion surrounding the creation of an Anthropocene Epoch; the shell middens built throughout history greatly influenced both estuarine ecology and landscapes through fishing and engineering practices.

1. Introduction

Conservation paleobiology and conservation archaeobiology, two subdisciplines of historical ecology, are relatively young pursuits within the Earth and environmental sciences. These fields recognize the value of using geohistorical data, those that predate written language and depend upon paleoecological and archaeological databases, for addressing modern problems of environmental management and conservation (Dietl and Flessa, 2011; Conservation Paleobiology Workshop, 2012; Rick and Lockwood, 2013). Methods and concepts that are more typically used by paleontologists and sedimentologists for interpreting deeper paleoenvironmental history are employed to infer the environmental conditions of the pre-human- or early-human-influenced past. These inferences then provide targets for environmental management and restoration (Kidwell, 2009; Conservation Paleobiology Workshop, 2012). Conservation paleobiology has also provided yet another perspective, along with the work of historians, anthropologists, and archaeologists (e.g., Denevan, 1992; Cronon, 1996; Balée and Erickson, 2006), on the false assumption that the pre-industrialized world was virtually pristine and natural. The baselines that environmental managers are seeking may have shifted one or more times through aboriginal and colonial human history (Pauly, 1995; Jackson et al., 2001). Pre-industrialized human societies, even those with small-scale

economies, had capacity to grossly alter natural conditions through such activities as habitat alteration, hunting, and fishing (Willis and Birks, 2006; Newsome et al., 2007; Knowlton and Jackson, 2008; Rick and Lockwood, 2013; Thompson and Waggoner, 2013; Boivin et al., 2016). Recognition of these effects has furthered the discussion over the creation of an Anthropocene Epoch and the timing of its onset (Smith and Zeder, 2013). Significant human effects on the geology and ecology of the planet do predate the Industrial Revolution (for elements of that discussion see: Crutzen, 2002; Zalasiewicz et al., 2008; Erlandson, 2013). Regardless of the timing of human-induced ecological change, environmental managers should be aware of these shifting baselines before designing and implementing restoration projects or management plans. Restoration targets must be accurately determined.

Numerous cases have documented humans overharvesting natural resources. The “overkill hypothesis,” which credits the extinction of megaherbivores and flightless birds to hunting, is now a well-accepted explanation for the many occurrences of end-Pleistocene / early Holocene extinction, though more recent analyses have noted that other anthropogenic drivers beyond over-hunting (i.e., habitat alteration) often had synergistic effects and that predation alone cannot be a universal driver of all megaherbivore extinction (Grayson, 2001; Barnosky et al., 2004; Miller et al., 2005; Koch and Barnosky, 2006; Grayson and Meltzer, 2015). The timing of extinctions on island continents and isolated landmasses often correlates remarkably well with the arrival of humans within that region (Burney and Flannery, 2005; Miller et al., 2005). In more recent history, industrial-scale fishing has decimated reefs in the Caribbean and the Great Barrier Reef of Australia by removing large herbivorous fishes, leading to shifts in

dominant species and, in some cases, trophic collapse (Jackson, 1997). Similarly, the commercial oyster fishery in Chesapeake Bay, which began in colonial times, has decimated the species, which in turn has caused great consequences for the ecology of the bay (Newell, 1988; Lenihan and Peterson, 1998; Kirby, 2004). Oysters were once prolific in New York Harbor, supporting one of the largest commercial oyster fisheries in the United States until the early 1900s, when anthropogenically driven habitat degradation and overharvesting eventually collapsed that fishery (Franz, 1982; Kurlansky, 2007). Lotze (2010), in her review of human-induced effects on U.S. estuaries, documented the extensive loss of oysters due to harvesting and habitat degradation in estuaries throughout the species' range along the Atlantic and Gulf of Mexico coasts. Human overharvesting can have profound evolutionary effects. Predation by humans, because of the species' effectiveness at removing large numbers of reproductive-aged adults, can drive rapid and intense phenotypic change in its prey species. These rates outpace those caused by natural agents, including those caused by other predators (Darimont et al., 2009).

Southwest Florida (USA) has supported a productive oyster reef ecosystem beginning about 3500 years ago (Savarese et al., 2004; Volety et al., 2009a). This ecosystem historically has been critical to the region's estuarine ecology for carbon fixation, trophic transfer, and natural water filtration (Tolley et al., 2003; Volety et al., 2009b). Additionally, the growth of oyster reefs has led to coastal progradation and the development of seaward coastal landforms during the same time interval. Oyster growth and reproduction has exceeded the rate of sea-level rise, which has transformed reefs into mangrove-forested islands and created new estuarine landmasses and barriers (Parkinson, 1989; Savarese et al., 2004). Despite this array of ecosystem services, no commercial

fishing industry for *Crassostrea virginica* (the eastern oyster) has ever existed in Southwest Florida. Nor has disease significantly influenced the region. Although the parasite *Perkinsus marinus* that causes the disease Dermo markedly increases *C. virginica*'s mortality and depresses reproductive success elsewhere throughout its range, the disease is inconsequential in these subtropical waters. The cool water temperatures in winter, paired with the low salinities of the summer, wet season, keep the rates of disease incidence low (La Peyre et al., 2003; Volety, 2008). Two anthropogenic drivers have principally produced harm: loss of suitable habitat due to development of coastal bays, and freshwater management. For the latter, much of Southwest Florida was re-plumbed through canalization to shed excessive freshwater into estuaries to avoid property damage. For this reason, estuaries suffer from water quality issues, where the principal pollutant is excessive freshwater. The restoration of the Greater Everglades focuses principally on restoring the natural hydrology through wetlands and estuaries, and oysters serve as a sentinel for restoration planning and a metric for restoration success (Barnes et al., 2007; Savarese and Volety, 2008; Volety et al., 2014). Additionally, restoring the habitats of oyster reefs to the estuarine-scape has become a priority for many states along the Atlantic and Gulf of Mexico coast, both to improve estuarine ecosystem services and to ensure this barometer of ecosystem health remains. (See Luckenbach et al. [1999] for a review of oyster reef restoration practices and purposes.)

To most effectively implement the restoration of oyster reefs in the region, knowing if oyster productivity has shifted significantly since pre-industrial time is necessary. For Southwest Florida, this potential shift likely occurred in the early to mid-20th century, when water management began and human population increased

significantly. Or, did aboriginal people, the Calusa and their predecessors who lived on this coastal landscape from 5000 BC to AD 1700, shift the oyster productivity baseline earlier in history? These Native Americans were significant consumers of the eastern oyster throughout Southwest Florida. The Calusa-generated mounds, composed of large volumes of oyster shell, found in virtually all Southwest Florida estuaries, suggest that overharvesting may have occurred.

Restoration success requires a firm understanding of oyster productivity before notable human influence. For this reason, an historical ecological approach to the problem that considers the possibilities of shifting baselines due to pre-industrial human influence is logical and invaluable. The oldest oyster reefs discovered through sediment coring in Southwest Florida date back to approximately 1200 BC (Parkinson, 1989; Savarese et al., 2004), during times when human population levels were relatively low (Archaic periods), through the Cal periods, including those of Calusa polity, when the Spanish arrived in the 16th century and the Calusa were extirpated, and up to the present. By combining paleoecological and archaeological data, the history of oyster productivity can be reconstructed (Rick et al., 2016).

This study addresses two research questions: (1) Did the Calusa and their predecessors over-exploit their oyster resource enough to influence the population structure and productivity of oysters? And (2) did overharvesting impose a lasting effect on oyster populations? If so, then the genetic composition of modern oyster populations is significantly different than the pre-anthropogenic populations, potentially handicapping restoration practices. The investigation employs oyster shells deposited within archaeological middens. Consequently, the validity of the study assumes that oysters

were collected alive for consumption, rather than as dead mound-building material or cultch. If the archaeological strata within the middens are composed of cultch, then oysters were not harvested and no impact on oyster population dynamics could result. Though few archaeologists question this assumption, this study at its onset tests the assumption of “collection for consumption” by employing a technique from paleobiology called taphonomic grading (Brandt, 1989, and described below).

2. Calusa Society

The Calusa were a complex fishing-gathering-hunting society that inhabited the region’s estuarine and barrier islands as well as some mainland shorelines (Marquardt, 2004). Although the Calusa exerted influence over much of South Florida by the 16th century, their heartland centered on the Pine Island Sound (PIS) and Estero Bay (EB) areas. In the PIS area, people periodically left behind middens on Useppa Island, first during the Middle Archaic cultural period, 5000-2000 BC, and continuing through Late Archaic (LA) times, 2000-500 BC (Marquardt, 1999). Another LA site, dated toward the end of the LA time range, is Calusa Island. With human population increase, some or all of the subsequent Caloosahatchee (Cal) I through V periods are represented at Useppa and many other sites. Based on site patterning and ethnohistoric documents, the Cal IV (AD 1350-1500) and part of the 16th century (earlier part of Cal V) represent times of peak Calusa population. The two largest population centers during this late time were Mound Key in EB and Pineland on Pine Island in PIS.

Unlike most other socially and politically complex pre-Columbian societies in North America, the Calusa did not rely upon agriculture for a storable food surplus (plant

foods, however, did contribute to their diet; e.g., see Newsom and Scarry, 2013).

Although their subtropical estuarine environment technically could have provided fish and shellfish on a year-around basis, surpluses would have been needed for bad times and for supporting those not fishing, such as laborers involved in large-scale projects. Among the diverse fishes available to the Calusa (Walker, 1992; deFrance and Walker, 2013), only mullet are both large and aggregate (during spawning episodes) in substantial numbers to allow mass capture, processing, and storage. Even so, mullet were not a main target until the latest Cal time periods. In contrast, of the shellfish options, the eastern oyster had been a staple food, complementing a variety of fishes throughout all time periods, although it occurred in smaller numbers in eastern PIS as evidenced by the molluscan assemblages from archaeological sites in the area (Walker, 1992; deFrance and Walker, 2013).

3. Study Areas and Samples

This study tested the assumption of “collection for consumption” and the question of overharvesting and its effects in two estuaries: Pine Island Sound and Estero Bay. These estuaries have had prolific oyster reef development coeval with human habitation through the late Holocene. Archaeological material (12 samples) came from four sites (Table 1), one within EB (Mound Key) and the other three within PIS (Fig. 1). For all but two samples (Useppa SR M-1-71 and Calusa Island NB Cs1a), details of excavation contexts, associated artifacts, radiocarbon dates (reported as one-sigma calibrated ranges), and sample assignments to cultural periods can be found in Torrence et al.

(1994), Marquardt (1999), Marquardt and Walker (2013), and Thompson et al. (2016).

The subsequent section describes the radiocarbon dating methods used for all samples.

All immediate sample contexts are midden deposits, although in two cases (Mound Key's L-1-9 and M-1-35), aboriginal construction activities likely moved the midden.

Mound Key (8LL2), a 125-acre (51-hectare) mound complex fringed by mangrove wetlands, is centered in EB and influenced by freshwater from the Estero River just to the northeast, and marine Gulf waters via the San Carlos Pass to the southwest. Mounds 1 (M1) and 2 (M2) are enormous, in large part composed of shell midden, and separated by a canal that leads to a central water court (W1). Sample C-1-94 (AD 588-686, Cal IIA-early) came from a southeastern extension of M1 (Torrence et al., 1994). Sample L-1-9 (AD 695-763, Cal IIA-late) is from M1, and sample M-1-35 (AD 990-1050, Cal IIB-late) is from M2 (Thompson et al., 2016). Sample D-1-95 (AD 1050-1169, Cal IV) is from the midden edge of W1 (Torrence et al., 1994). To date, all of the excavated Mound Key molluscan shell assemblages are dominated by oyster shell, a reflection of the island's setting.

Useppa Island (8LL55), roughly 1.7 km long and 0.5 km wide, is in western PIS, just east of the barrier island, Cayo Costa. Owing to a core of high Pleistocene-age dunal sands, the overlying archaeological deposits on the island include the oldest in the region (Marquardt, 1999). Sample B-13-15 (2000-1860 BC, LA) is from a pre-ceramic shell midden in the central area atop a ridge locally referred to as Calusa Ridge (CR). Sample D-3-4 (AD 1-180, Cal I-late) is from a midden not far to the north on the same ridge. At these locations, the midden shells are a little more diverse than those at Mound Key, although the eastern oyster is still the most abundant taxon represented. (Useppa's Cal

IIA and IIB assemblages, however, are much more diverse [no oyster samples included in this study.] Sample M-1-71 (1180-1040 BC, LA) is from a shell midden buried by dunal sand located in the southern part of Useppa on what is known as Southern Ridge (SR). This LA midden contains early pottery and its molluscan shell assemblage again includes oyster as the most abundant. It differs from the other Useppa samples though, in that the assemblage as a whole indicates a much higher salinity environment.

Calusa Island (8LL45) lies just off the north end of Pine Island. Its only upland area (0.03 km²; 8 acres) is defined by an extensive shell midden, much of which dates to the latest LA, sometimes referred to as the Terminal Archaic. Sample Cs1a (785-745 BC) came from a vertical section at the site's North Beach (NB) where the midden is actively eroding. The overall shell assemblage at this site, unlike the others, has not been quantified, but visually is overwhelmingly oyster.

The Pineland Site Complex (8LL33, etc.), at 0.26 km² (65+ acres), is located prominently on the northwestern shoreline of Pine Island. Like Mound Key, it consists of multiple mounds, ridges, and waterways with two large mound complexes separated by a canal (Marquardt and Walker, 2013). Its estuarine waters are part of the eastern PIS, characterized by shallow-water and expansive seagrass meadows, which are preferred habitats for many marine gastropods. Freshwater input is limited. With few exceptions, Pineland's shell middens exhibit great numbers of gastropod shells and relatively few oyster (and other bivalve) shells. Oyster samples A-8-101 (AD 110-270, Cal I-late-f), A-16-94 (AD 270-420, Cal I-late-i), and A-16-92 (AD 530-630, Cal IIA-early-a) are all from middens below Pineland's Old Mound. Sample I-2-66 (AD 1270-1330, Cal IV) is from Mound 2 within the Brown's Complex (BCM2). Although this sample's

radiocarbon date is just under the Cal IV range of AD 1350-1500, the pottery assemblage is clearly indicative of IV, and the two-sigma range of the date pushes it to AD 1400.

The twelve archaeological samples span a time period from 2000 BC to AD 1500, and include several climatic cool and warm intervals (Table 1). For the basis of these climate-episode assignments, we refer readers to the reviews, discussion, and referenced literature presented in Marquardt (1999) and Marquardt and Walker (2013). This temporal range considers harvesting effects during times of low (LA) and dense human populations (Cal). It also allows exploration of the effects of environmental conditions, rather than fishing practices, on oyster productivity (i.e., climate's effect upon oyster growth).

In addition, death assemblages (i.e., collections of dead oyster shells; definition after Fürsich, 1990) were collected from four modern oyster reefs neighboring the archaeological sites (Table 1). Though certainty cannot be established, these modern reefs may have served as oyster fishing grounds for the aboriginal inhabitants. The Horseshoe Keys reef region (Hs) is approximately 2 km² in size and adjacent to Mound Key in EB. Useppa Reefs 1 (1.25 km²) and 2 (0.5 km²) (Us1, Us2, respectively) are found just north and south of Useppa Island and west of Pineland. The Calusa Island Reef (0.3 km², Cs) is a short distance from the Calusa Island archaeological site. Though the histories of the Us1, Us2, and Cs reefs have not been studied geologically, through sediment coring, the Horseshoe Keys reef has stratigraphy that dates back to Cal BP 2675 (Wohlpert, 2007; Wohlpert et al., 2007). Figure 2 illustrates a stratigraphic column of a sediment core taken from Horseshoe Keys. Radiocarbon dates of shells taken from beds representing the onset of reef development are aged at Cal BP 2195. These reefs clearly

have a deep enough temporal history to have been an active harvesting area for the Calusa residing on Mound Key. These four death assemblages allow comparison among archaeological and modern oyster populations, both for oyster productivity and growth rate, and for taphonomic grade.

4. Methods

4.1 Archaeological Samples

Samples from archaeological sites came from bulk samples curated by the Florida Museum of Natural History. Seven of these samples were analyzed completely; all invertebrate and vertebrate animal remains were identified and quantified. The samples were excavated during many field projects over a span of time ranging from 1989 to 2014. Most were excavated in the same manner: 50x50x10-cm areas of midden were selected from distinct strata (i.e., no mixing of different strata), and material was removed by trowel and dust pan, bagged, and later screened. The Calusa Island sample is the exception. It was collected from a 45-cm thick horizon within a well-defined bed confined between two paleosol surfaces, exposed on a wave-cut scarp along the Pine Island's North Beach. Each bulk sample contained approximately 500 individual oyster valves.

Bulk samples were randomly subsampled to amass a collection of 100 oyster left valves (hereafter referred to as the “convex”, rather than the right, “cap” valve). Those valves that were severely fragmented were discarded because length could not be measured and taphonomic grade of the shell interior could not be assessed.

4.2 Modern Reefs

Oysters from the modern reefs were collected using a line transect – point intercept method (Henderson, 2003). A tape measure was stretched across a low tide-exposed reef surface along the reef’s most productive topographic contour. At regular intervals (every 5 or 10 cms, depending upon the length of the transect), the closest dead oyster convex valve located at the intercept point was collected. Valves that were less than 2 cm in length were avoided. As with the archaeological samples, any valve that was fragmented significantly to prevent the measurement of length was also discarded. This sampling scheme provided a minimum of 100 convex valves for each locality.

In addition, 25 living oysters of various sizes were collected from each modern reef to establish an allometric relationship between the length of oyster convex valves and wet tissue biomass. (Twenty-five oysters are sufficient to describe the shape of the allometric relationship.) To obtain wet tissue biomass, the mass of each oyster shell was subtracted from the animal’s complete mass. Plotting convex shell length (see method below) against wet tissue biomass, a best-fit power function was generated for each reef and compared.

4.3 Radiocarbon Dating

Standard radiocarbon dating provided ages of the archaeological samples for non-oyster, co-occurring mollusk species (Table 1). Beta Analytic, Inc., performed the dating for 10 specimens; University of Georgia’s Center for Applied Isotope Studies (CAIS-UGA) provided the ages for 2 samples (Mound Key L-1-9 and M-1-35). Nine specimens

were shells of the southern quahog clam (*Mercenaria campechiensis*), two were of the lightning whelk (*Sinistrofulgur sinistrum*), and one was a marine shell of unrecorded taxon.

4.4 Taphonomic Grading

Taphonomic grading is the qualitative scoring of a shell's preservational state. It reflects the post-mortem history of the shell after soft tissue loss or decay of the soft tissue (Brandt, 1989; Kowalewski et al., 1995). Paleontologists commonly use taphonomic grading as a proxy for spatial and temporal fidelity (Flessa et al., 1993; Meldahl et al., 1997; Kowalewski et al., 1998): the better the preservational state, the less likely the shell remained exposed on the seafloor for long periods of time before final burial. A pristine shell with a high quality grade should have been removed from the post-mortem environment, either by burial or, for this study, by consumption soon after death.

Shells can degrade because of physical, chemical, or biological factors (Lawrence, 1968; Behrensmeyer and Kidwell, 1985). Of these factors, biological degradation (i.e., encrustation or biocorrosion) typically occurs in a subaqueous, marine or estuarine environment. An oyster that was collected alive in an estuarine setting, shucked, consumed, and discarded on a shell midden would have a well-preserved biological taphonomic grade on its shell interior. An oyster that had died naturally on a reef would have its shell interior degraded by biological agents. Physical and chemical agents can degrade shells both in subaqueous and subaerial conditions. Consequently, only biological grade was assessed, and only on the interior of the convex valves.

Biologic taphonomic grades were scored as shown in Table 2; Figure 3 shows photographic representations of the four grades. A grade of 1 represents a pristine shell; a grade of 4 is most degraded. Three trained persons graded each valve interior independently, providing an average grade for the analysis. Physical and chemical taphonomic grades were also scored for all shells, but those data are not reported herein.

4.5 Oyster Valve Morphology

Valve length (also known as height) and width (Fig. 4A) were measured to the nearest millimeter using digital calipers. Length is defined as the longest axis of the convex valve from the hinge's umbo to the growing margin; width is the largest distance perpendicular to shell length. Cap valves were also collected and measured. Data for shell widths and for cap valves are not reported herein but are available from the authors.

Accretionary growth lines or annuli can serve as a proxy for age if the growth lines are produced with seasonal periodicity. The age of oysters can be obtained by counting growth lines exposed within the ligament hinge pit of the convex valve (Fig. 4B) (Stenzel, 1971). Though oysters grow through accretion, annuli within the body of the shell are difficult to discern and therefore unreliable indicators of age (Carriker, 1996). Calcium carbonate within the ligament hinge pit is also accreted with annual periodicity, and the annuli here are more readily observable (Carriker, 1996). In temperate waters, *C. virginica* exhibits growth stoppage during the colder winter months, producing one growth band per year (Kirby et al., 1998; Andrus and Crowe, 2000; Kirby and Miller, 2005; Fan et al., 2011). In warmer, subtropical waters, like those found in Southwest Florida, oysters may halt growth in the winter, if cold conditions prevail, or in

summer, if water temperatures get too hot (Surge et al., 2001). These climatic conditions can result in 0-2 growth bands in a year.

Growth rate (the relationship between shell length versus growth line) was obtained for 8 populations of oysters, spanning the LA (M-1-71, Cs1a), Cal (C-1-94, L-1-9, M-1-35), and modern periods (Us1, Us2, Hs). Between 17 and 42 oysters were analyzed for each population; the number of individuals varied considerably between samples because of marked differences in the preservational state of the ligament pits. Growth bands were exposed by cross sectioning the convex valve's ligament pit parallel to the growth direction (Fig. 4B). Three investigators counted the number of translucent growth bands from the umbo to growing edge independently for each convex valve, producing a mean value. The three investigators obtained comparable counts, typically falling within ± 2 growth lines. Convex shell length was plotted versus number of growth lines for each oyster population.

4.6 Statistical Methods

JMP 12 provided the software testing statistical relationships. Significance was tested at the $\alpha = 0.05$ level as follows. For biologic taphonomic grade, samples were combined into three groups: Late Archaic, Caloosahatchee, and modern death assemblages. The former two groups represent archaeological midden samples, whereas the latter represents the taphonomy of oysters collecting after death on modern reefs. A chi-squared contingency analysis was conducted using both Likelihood Ratio and Pearson tests for the 3 groups. In addition, the three groups were compared for taphonomic grade using nonparametric Wilcoxon pairwise tests. To compare convex

valve length among the 16 archaeological and modern samples, shell lengths were first log-transformed to achieve normal distributions. ANOVA then provided comparisons. Best fit linear functions of shell length versus growth lines were generated for each of the 8 populations. Valve lengths were log-transformed to generate normal distributions, and then the slopes and y-intercepts of the populations were compared using an ANCOVA.

5. Results

5.1 Taphonomic Grading

The biologic taphonomic grades of the modern reef death assemblages tend to be poor, with means ranging from 1.69-2.50 (Table 3). Scores of this magnitude represent valve interiors that have up to 75% of their surfaces covered by bioeroders or encrusters. Figure 5A shows a sample histogram from the modern reef at Horseshoe Keys in EB. In contrast, the taphonomic grades of archaeological samples are considerably better with means as low as 1.18 (Table 3). For example, sample M-1-35 from the Cal IIB-late period at Mound Key, EB, has a distribution with a mode of 1, a pristine grade, and a mean of 1.26 (Fig. 5B). Overall, samples from modern reefs are less positively skewed than the archaeological samples (Table 3).

Chi-square contingency analysis of the 3 sample groupings (Late Archaic, Caloosahatchee, and modern) shows that both archaeological groupings have a greater likelihood of a taphonomic grade of 1, while the modern death assemblage grouping does not (both via Likelihood Ratio and Pearson tests, $p < 0.0001$). Nonparametric Wilcoxon pairwise comparisons show that the modern group has a poorer grade than both the Late

Archaic and Caloosahatchee groups ($p < 0.0001$). The Late Archaic is slightly different from the Caloosahatchee group ($p = 0.017$) (Fig. 6).

5.2 Oyster Valve Length

Convex valve lengths for the 4 modern reef death assemblages have mean values ranging from 54.5-66.4 mm, whereas means for the 3 LA archaeological samples range from 52.5-79.7 mm. The 9 archaeological samples from the Cal cultural period all have smaller means, ranging from 34.2-50.7 mm, than both the LA and modern samples (Table 4). Figure 7 shows sample means and standard errors arranging chronologically from oldest to youngest and the climatic periods in which they were formed.

After the data are log-transformed and subjected to ANOVA, the samples group statistically in revealing ways (Fig. 8). Cal samples group most commonly among themselves, and these samples are almost exclusively smaller in size than the groups forming among the LA and modern samples. Groups E and F (Fig. 8) have member samples that are found either in both the Cal and LA groups or between the Cal and modern groups. Groups B, C, D, and E have members among both the LA and modern samples, indicating that the oldest and youngest oysters are comparably sized.

5.3 Modern Oyster Productivity

Oysters within the two modern estuaries, EB and PIS, have very similar positive allometric relationships between convex shell length and wet tissue biomass. Best fit power function regressions for three populations of living oysters (from Horseshoe Keys in EB; Calusa Island, northern PIS; and Useppa Island in central PIS) have scaling

exponents between 2.3-2.6 (Fig. 9). These exponents indicate that convex shell length is a reasonable proxy for productivity.

5.4 Oyster Growth Rate

The slope of the relationship between ligament pit growth lines and shell length served as a proxy for the rate of oyster growth. The method generated results for 8 samples (2 LA samples [Cs1a, M-1-71], 3 Cal samples [C-1-94, L-1-9, M-1-35], and 3 modern reefs [Us1, Us2, Hs]) (Fig. 10). An ANCOVA of the log-transformed data demonstrates that, although the y-intercepts of the 8 linear regression functions are different ($p < 0.0001$), the slopes are indistinguishable ($p = 0.3302$).

6. Discussion and Conclusions

Although an erroneous assumption that the Calusa and their predecessors harvested oysters live for consumption before discarding shells on a midden would obviate this entire study, the analysis of biological taphonomic grade supports that assumption. Oysters found within the archaeological samples have well preserved shell interiors. Shells left on the bay floor after death quickly degrade after the valves disarticulate and the soft tissue of the oyster is consumed or decays. The significantly poorer grades and the less positively skewed distributions for modern reef death assemblages attest to this phenomenon. The subaerial environment of an oyster shell discarded after consumption would not support biological degradation. Although exposure to air or fresh, meteoric water might physically damage a shell through

fracturing or chemically alter its composition and luster, the biological agents responsible for biocorrosion, boring, and encrustation require an estuarine or marine aquatic environment. Using similar logic, Henderson et al. (2002) distinguished death assemblages of *C. virginica* in a shell midden from those in a chenier plain based on chemical taphonomic grades. Oysters deposited on a chenier are exposed to aquatic conditions, while those in the midden are not. The latter exhibited greater chemical degradation.

Similar comparisons of taphonomic grade have been used to recognize time averaging after death of marine and estuarine shellfish within fossil assemblages (Meldahl et al., 1997; Kowalewski et al., 1998). Though the rate of taphonomic degradation can vary widely between environments and among different taxa, when these variables are controlled, longer residence times of death assemblages on the seafloor (i.e., the greater the time averaging) lead to poorer preservational state (Kidwell, 1998; Powell et al., 2002; Callender et al., 2002). Although a shell may remain pristine for long periods of post-mortem exposure in marine and estuarine settings, the pervasiveness of pristine taphonomic grades supports live harvesting.

Interestingly, the mean taphonomic grades for the archaeological samples are not invariantly equal to “1”. The means are somewhat larger, indicating that some shells within a midden’s sample have been degraded biologically. This result likely reflects the phenomenon of inadvertent “bycatch” of dead shells while live animals are collected. Young oysters recruit and cement to adults through reef history, causing oysters to clump. Consequently, a clump will consist of both living and dead individuals. Modern oystermen, when raking reefs, will inadvertently collect dead along with living oysters.

These fishermen cull the clumps and return as much of the dead bycatch as possible, but, no doubt because the process is time consuming, dead individuals return to the dock with living individuals (Keiner, 2009). The inclusion of oysters with non-pristine biological taphonomic grades on the shell interior may reflect similar shellfishing practices by the Calusa and their predecessors. Thorough culling at the reef site would be time consuming. Alternatively, storage space on a canoe is limiting. The Calusa would have wanted to minimize the volume of bycatch transported back to the midden.

With respect to shell size, the statistical analysis demonstrates that LA and modern oysters are significantly larger than their Cal counterparts. This phenomenon is upheld regardless of the climatic phase – whether within a climatic cool or warm period. During those phases of the Cal periods represented by the samples available (Caloosahatchee I through IV; AD 1-1500), the human population size in the region was significantly greater than during the preceding LA (2000-745 BC) (Marquardt, 2014). This decrease in mean oyster size when human population was high is interpreted as a consequence of overharvesting. Demands on the shellfishery were greater during this time, and extensive harvesting drove the mean oyster population size downward. Significant variation existed, however, in the mean size of oysters among samples from the Cal period, further suggesting that the stress of overharvesting varied throughout this time interval. The Caloosahatchee people may have preferentially removed larger individuals from clumps at the time of collection. Modern oystermen, using traditional hand-tonging practices, undertake this practice. They use tongs to bring clumps onboard their vessels, they cull the clumps to remove marketable individuals, and then return the smaller living individuals and dead bycatch to the water (Chesapeake Bay, 2002).

Numerous climatic fluctuations occurred throughout this history, and the effects climate might have had on estuarine conditions could have caused the changes observed in the productivity of oysters. It is reasonable, however, to assume that patterns of temperature and precipitation change were repetitive in nature, restoring comparable estuarine conditions to previous states. The fact that the pattern of shell size reduction is maintained through two intervals of warming-cooling suggests that climate did not induce estuarine change.

Results further suggest that even though overharvesting occurred, those fishing practices did not influence the portion of the oyster's genotype affecting growth rate. With ligament pit growth lines as a proxy for age, the slopes of convex shell length versus growth line linear regression functions are indistinguishable statistically when LA, Cal, and modern populations are compared. Elsewhere in *C. virginica*'s biogeographic range, anthropogenic drivers have caused negative shifts in oyster growth rate. Oysters consumed by colonists at Jamestown, Virginia (1611) had significantly faster growth rates than modern oysters from the same estuary. The authors Harding et al. (2008) credited this shift to both increasing temperatures and the human introduction of modern diseases. A subsequent study demonstrated that this reduction in growth rate, coupled with the age-truncated mortality that accompanies the disease Dermo, is reducing *C. virginica*'s reef-building capacity to keep pace with sea-level rise throughout Chesapeake Bay (Mann et al., 2009). Given the oyster's role in the development of Southwest Florida's coast, any lasting anthropogenic impact on the growth of oysters could have profound implications for the region's future coastal geomorphology and estuarine ecology.

The use of ligament pit growth lines as a proxy for age is well established for *Crassostrea virginica* living in temperate waters (Andrus and Crowe, 2000; Kirby and Miller, 2005). Oysters in these estuaries exhibit a stoppage of growth typically just in the winter, when water temperatures are low, and not in the summer, thereby producing one growth line per year. Subtropical oysters, however, are somewhat more problematic (Kirby et al., 1998; Surge et al., 2001). In these warmer climates, an oyster may exhibit growth stoppage in the winter, if cooler temperatures prevail, and may stop growth in the summer if estuarine waters become too warm. This trend adds greater variability to the number of growth lines that can be produced in a calendar year. Consequently, the validity of this result may be tentative, which warrants further testing that was beyond the scope of the present study. Two design approaches might be used in future studies. One, an increase in oyster sample size per time interval and locality would increase the robustness of the analysis. More oysters could be sectioned and their growth lines counted. Second, *C. virginica* does exhibit a seasonal cyclicity in the stable oxygen and carbon isotopes that are encoded in the precipitated calcium carbonate of the hinge ligament pit. Such patterns have been revealed in oysters of Southwest Florida (Surge et al., 2001, 2003). Growth lines then can be calibrated against this cyclic geochemical signal, thereby allowing the assumption to be further tested.

Assuming the worst and the ligament growth line data from this study are flawed, the fact that oyster size is restored to LA magnitudes on modern reefs (i.e., the shell length dataset) is sufficient to conclude that the genetic capacity of *C. virginica* was not unduly and permanently altered by Calusa shell harvesting. If the growth line data are genuine, the conclusion is reinforced. Additionally, *C. virginica* is consistently the most

common shellfish taxon among all archaeostrata within Mound Key (throughout Cal history). No indication exists that oyster abundance or availability changed because of Calusa harvesting. Though this study did not evaluate patterns in abundance among the archaeological assemblages, this observation further supports anecdotally the absence of a permanent change in population genetics.

Though Calusa and their predecessors had a varied diet, oysters were a common food and a principal component of their diet. The volume of oyster shell within the middens attests to this prominence. Data revealed in this study indicate that overharvesting of oysters did occur, that fishing practices did influence the population structure of the species, but did not impose a lasting evolutionary shift in the species' capacity to grow. The oyster populations were resilient.

Overharvesting of shellfish by aboriginal people has been documented in other cultures. In some cases, overharvesting caused temporary demographic shifts that later showed recovery, as with this study; in others, overharvesting caused significant genotypic changes or local extinction. The overexploitation of hard clams (*Mercenaria* spp.) by pre-Columbian people in coastal areas of the state Georgia and eastern-central portions of Florida was common between 2500 BC – AD 1500. Using incremental accretionary growth bands to age clams, a significant reduction in *Mercenaria*'s mean ontogenetic age was documented among zooarchaeological samples. These shifts correspond geographically with areas of dense aboriginal human population. In the same regions today, mean ages of modern *Mercenaria* populations are significantly higher, demonstrating that the overharvesting ontogenetic shift was temporary (Quitmyer and Jones, 2000; Quitmyer and Jones, 2012). In three case studies on oyster resource

exploitation during the Mesolithic-Neolithic transition in Demark, Milner (2013) found clear evidence of human impacts on oyster beds in terms of a decrease in size, as well as a decrease in age of capture. Despite the impacts of harvesting on these oyster populations, they did not become locally extinct and populations did recover (Milner, 2013). Erlandson et al. (2008) investigated the impact of Native American shellfishing throughout a 10,000-year record from San Miguel Island, California, and demonstrated that overharvesting resulted in the reduction of mussel and red abalone shell size. Throughout this protracted interval of Native American fishing, the shellfish populations remained sustainable through the Holocene, suggesting that permanent and significant genotypic change did not occur.

Other studies of aboriginal shellfishing show more significant influence on population genetics. Using a conservation paleobiological approach employing paleontological, archaeological, and modern ecological data, O'Dea et al. (2014) documented a case of intensive size-selection harvesting of the edible, fighting conch, *Strombus pugilis*, in the western Caribbean that resulted in a reduction in size of sexual maturity. A reduction was noted first from pre-human time (at 7000 years ago) to prehistoric time (at 1000 years), and again up to modern times. A comparison of modern and pre-Columbian bay scallops (*Argopecten irradians*) from Florida's central and southern Gulf of Mexico coast showed that abrupt shifts in shell morphology occurred sometime between 500-1500 years ago (Marelli and Arnold, 2001). Those morphological changes are retained in today's populations, suggesting that overharvesting drove a permanent genotypic change within local populations. Interestingly, one of the

archaeological midden sites included in the study of Marelli and Arnold (2001) was from Pineland, from the same span of Calusa history investigated in this research.

The pattern identified in this study for *Crassostrea virginica* in Southwest Florida is not unique, but it does contribute to a growing body of evidence for aboriginal human impact on estuarine systems, particularly where shellfishing forms the economic basis of production (Thomas, 2014). Additionally, it is relevant for the debate surrounding a formal adoption of the Anthropocene Epoch. As Erlandson (2001, 2013) noted, the widespread practice of intensive shellfishing occurred during the Holocene. He argued that the emergence of large-scale shell middens, along with other forms of anthropogenic sediments around the world, could be viewed as a “clear signature for an Anthropocene Epoch” (Erlandson 2013:30). Erlandson also argued that the creation of these sediments alters the landscape on a number of levels including topography, soil chemistry, and hydrology, thus offering many prospects for unique plant and animal communities to colonize these areas (Erlandson, 2013; see also Boivin et al., 2016). Additionally, findings from this study suggest that the creation of shell middens is more than the sum of the visible shell left behind, but also leaves lasting effects imparted on the estuarine communities of a given region. Thus, human impacts are present both above and below the waterline in areas where indigenous communities practiced shellfishing. This fact has implications for how to evaluate the amplitude of past human impacts, as many are not obvious on the landscape (Thompson, 2013), as well as to detect exactly when humans began altering the processes of Earth systems, and for how “pristine” environments are defined. Such perspectives are critical for managing contemporary ecosystems.

Results of this study demonstrate that the assumption of pristine estuaries existing in pre-industrial Southwest Florida is flawed, even given the late timing of modern societal development in the latter half of the 20th century. Native Americans, through subsistence harvesting of oysters, and perhaps of other shell- and finfish species (e.g., the bay scallop research by Marelli and Arnold [2001], discussed above), influenced the ecology and population structure of at least one estuarine ecosystem: oyster reefs. The history of *Crassostrea virginica* is easily accepted as unaffected by anthropogenic drivers from post-Columbian to pre-industrial time because commercial harvesting of the species in this region has not occurred. No markets for oysters from Southwest Florida have existed; the presumption that pre-Columbian fishing might have had an effect on the oyster's population ecology and genetics has not been considered before this investigation.

The biology and ecology of oysters have been more recently and severely influenced by contemporary anthropogenic drivers associated with modern water management and coastal development. These practices have severely reduced suitable substrate for the development of oyster reefs throughout Southwest Florida's estuaries because of growth in the housing, marina, and inland navigation sectors. The extent of reefs in Naples Bay, for example, has decreased by approximately 80% since pre-1950s due to loss of suitable habitat through waterway and marina development (Schmid et al., 2005). Merely relict areas of reef formation exist today (Dellapenna et al., 2013). Canals built for freshwater to avoid storm water flooding of upland suburban property and agricultural lands have altered the timing and quantity of freshwater delivery to estuaries. Before the 1980s, the draining of wetlands for human use had similar effects. These

cumulative influences degraded estuarine health and collectively resulted in a decrease in oyster productivity and reef areal extent (Savarese et al., 2003; Tolley et al., 2006).

Over the past 15 years, the restoration of oyster reefs has become a priority for regional and state environmental managers because of the ecosystem services they provide (e.g., water filtration, shoreline protection, trophic transfer of carbon, and promotion of biodiversity). Southwest Florida has supported numerous reef restoration efforts in many estuaries (including, from north to south, the Peace River, Caloosahatchee River, Estero Bay, Ccohatchee River, Naples Bay, and Rookery Bay National Estuarine Research Reserve; e.g., Rasnake et al., 2004; Savarese et al., 2007). These efforts have assumed that the estuarine conditions of the mid-20th century make suitable targets for restoration planning. Though this study demonstrates that baseline shifts have occurred in oyster productivity throughout deeper human history, restoration planning has not been compromised by that activity. Results from this study demonstrate that modern oysters exhibit the same population characteristics and growth rates as those on the estuarine-scape early in Native American history. The species has retained the capacity for productivity and growth despite the overharvesting by Southwest Florida's aboriginal people.

Finally, this study exemplifies the value of incorporating an historical ecologic approach to environmental science and management investigations. Archaeological data and paleontological methods often provide a unique opportunity and perspective for documenting shifting baselines in population ecology and evolution. These perspectives are invaluable for management and restoration planning.

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Figure & Table Captions

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Table 1. Archaeological samples and modern death assemblages used in the study.

Included are: the region (CR, Calusa Ridge; SR, Southern Ridge; NB, North Beach; OM, Old Mound; M1, Mound 1; M2, Mound 2; W1, Watercourt 1; BCM2, Brown's Complex Mound 2), site name, cultural period (LA, Late Archaic; Cal, Caloosahatchee), climatic interval (RWP, Rowan Warm Period; VM, Vandal Minimum; MWP, Medieval Warm Period; LIA, Little Ice Age), and age, based on

radiocarbon dating, and the shell material dated (*Mercenaria campechiensis*; *Sinistrofulgur sinistrum*).

Table 2. Criteria used to assign physical (fragmentation), biological (bioerosion/encrustation), and chemical (loss of luster/color) taphonomic grades. Only the biological taphonomic grade was used to evaluate the post-mortem history of oyster shells.

Table 3. Biological taphonomic grades. Samples span the Late Archaic and Caloosahatchee cultural periods, and the modern. Specific ages of the samples are listed in Table 1. The “Pearson’s moment coefficient of skewness” was used to obtain measures of each distribution’s skewness. All samples are positively skewed, but most archaeological samples are more so than most modern samples (shown in green), validating the interpretation of oyster harvesting for food; a small number of samples (in red) have skewnesses that counter this interpretation.

Table 4. Mean, standard error, minimum, and maximum for convex valve lengths (mm); sample size (N). Samples span the Late Archaic and Caloosahatchee cultural periods, and the modern. Specific ages of the samples are listed in Table 1.

Tables & Figures to follow . .

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Sample	Region	Site	Age	Material Dated	Cultural Period	Climate
B-13-15	Pine Island Sound	Useppa Island CR	2000-1860 BC	marine shell	LA-preceraemic	SB-cool
M-1-71	Pine Island Sound	Useppa Island SR	1180-1040 BC	<i>M. campech.</i>	LA-terminal	SB-cool
Cs1a	Pine Island Sound	Calusa Island NB	785-745 BC	<i>S. sinistrum</i>	LA-terminal	SA-warm
D-3-4	Pine Island Sound	Useppa Island CR	AD 1-180	<i>M. campech.</i>	Cal-late	RWP-warm
A-8-101	Pine Island Sound	Pineland OM	AD 110-270	<i>M. campech.</i>	Cal-late-f	RWP-warm
A-16-94	Pine Island Sound	Pineland OM	AD 270-420	<i>M. campech.</i>	Cal-late-i	RWP-cool
A-16-92	Pine Island Sound	Pineland OM	AD 530-630	<i>M. campech.</i>	Cal-LIA-early-a	VM-cool
C-1-94	Estero Bay	Mound Key M1	AD 588-686	<i>M. campech.</i>	Cal-LIA-early	VM-cool
L-1-9	Estero Bay	Mound Key M1	AD 695-763	<i>M. campech.</i>	Cal-LIA-late	VM-cool
M-1-35	Estero Bay	Mound Key M2	AD 990-1050	<i>M. campech.</i>	Cal-LB-late	MWP-warm
D-1-95	Estero Bay	Mound Key W1	AD 1050-1169	<i>M. campech.</i>	Cal-IV	LIA-cool
I-2-66	Pine Island Sound	Pineland BCM2	AD 1270-1330	<i>S. sinistrum</i>	Cal-IV	LIA-cool
Hs	Estero Bay	Horseshoe Keys	Modern		Modern	warm
Us1	Pine Island Sound	Useppa Reef 1	Modern		Modern	warm
Us2	Pine Island Sound	Useppa Reef 2	Modern		Modern	warm
Cs Reef	Pine Island Sound	Calusa Island Reef	Modern		Modern	warm

Table 2. Criteria used to assign physical (fragmentation), biological (bioerosion/encrustation), and chemical (loss of luster/color) taphonomic grades. Only the biological taphonomic grade was used to evaluate the post-mortem history of oyster shells.

Characteristic	Grade 1	Grade 2	Grade 3	Grade 4
1. Fragmentation	Complete margin	>75% margin	25%-75% margin	< 25% margin
2. Bioerosion / encrustation (shell interior)	None	<25% affected	25%-75% affected	>75% affected
3. Loss of luster / color (shell interior)	No loss of nacre or color	Nacre & color slightly faded	Nacre & color still present but faint	Complete loss of nacre and color

Table 3. Biological taphonomic grades. Samples span the Late Archaic and Caloosahatchee cultural periods, and the modern. Specific ages of the samples are listed in Table 1. The “Pearson’s moment coefficient of skewness” was used to obtain measures of each distribution’s skewness. All samples are positively skewed, but most archaeological samples are more so than most modern samples (shown in green), validating the interpretation of oyster harvesting for food; a small number of samples (in red) have skewnesses that counter this interpretation.

Sample	Cultural Period	Mean	Standard Error	Standard Deviation	Skewness
B-13-15	L Archaic	1.42	0.056	0.556	1.785
M-1-71	L Archaic	1.18	0.056	0.557	3.564
Cs1a	L Archaic	1.68	0.106	1.063	1.376
D-3-4	Caloosah	1.94	0.067	0.668	0.439
A-8-101	Caloosah	1.60	0.058	0.577	0.666
A-16-94	Caloosah	1.37	0.067	0.474	1.289
A-16-92	Caloosah	2.31	0.133	0.939	0.411
C-1-94	Caloosah	1.34	0.067	0.794	2.258
L-1-9	Caloosah	1.20	0.054	0.534	2.574
M-1-35	Caloosah	1.26	0.077	0.774	2.940
D-1-95	Caloosah	1.33	0.071	0.565	1.503
Hs	Caloosah	1.79	0.086	0.852	0.824
Us1	Modern	2.16	0.065	0.647	0.289
Us2	Modern	2.50	0.105	1.049	0
Cs Reef	Modern	1.69	0.088	0.875	1.246

Table 4. Mean, standard error, minimum, and maximum for convex valve lengths (mm); sample size (N). Samples span the Late Archaic and Caloosahatchee cultural periods, and the modern. Specific ages of the samples are listed in Table 1.

Sample	Cultural Period	N	Mean (mm)	Standard Error	Minimum (mm)	Maximum (mm)
B-13-15	L Archaic	100	52.5	1.099	30	83
M-1-71	L Archaic	97	59.9	1.646	31	104
Cs1a	L Archaic	86	79.7	1.699	45	118
D-3-4	Caloosah	100	50.7	1.142	30	86
A-8-101	Caloosah	100	47.5	1.362	21	104
A-16-94	Caloosah	50	34.2	1.119	17	56
A-16-92	Caloosah	50	41.4	1.383	26	73
C-1-94	Caloosah	100	46.7	0.978	20	73
L-1-9	Caloosah	99	48.5	1.187	26	81
M-1-35	Caloosah	83	44.4	1.011	26	70
D-1-95	Caloosah	47	42.0	1.513	21	68
Hs	Caloosah	97	66.4	1.668	26	115
Us1	Modern	100	56.7	0.999	37	100
Us2	Modern	100	58.8	1.170	25	85
Cs Reef	Modern	100	54.5	1.047	32	83

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