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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

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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).