Using the Fossil Record to Establish a Baseline and Recommendations for Oyster Mitigation in the Mid-Atlantic U.S.

Kristopher M. Kusnerik, Rowan Lockwood, and Amanda N. Grant

Abstract Eastern oyster populations throughout the Mid-Atlantic region of the USA have been in decline for centuries due to overharvesting, disease, increased sediment pollution, and habitat destruction. By studying Pleistocene fossil oyster assemblages, it is possible to reconstruct baseline conditions and develop recommendations for oyster mitigation. Fossil assemblages were studied from five Pleistocene sites located in Maryland, Virginia, and North Carolina. Reconstructions of paleosalinity and temperature were used to identify modern and colonial sites with similar environmental parameters for comparison. Shell height and life span in Chesapeake Bay oysters declined significantly from the Pleistocene to today, at the same time that ontogenetic growth rates have increased. This pattern is driven by age truncation, in which both harvesting and disease preferentially remove the larger, reproductively more active and primarily female members of the population. By contrast, Pleistocene oysters from North Carolina did not differ significantly, in shell height, life span, or growth rates, from modern oysters.

Although oyster management in the Mid-Atlantic States has focused historically on protecting and supplementing early life stages, this study recommends three potential management solutions to the age truncation revealed by comparison with Pleistocene oysters. Possible solutions include (1) implementation of a maximum size or slot limit on the fishery, (2) establishment of marine protected areas (MPA), or (3) significant lowering of exploitation rates.

K. M. Kusnerik (✉)
Division of Invertebrate Paleontology, Florida Museum of Natural History, Gainesville, FL, USA
e-mail: kmkusnerik@ufl.edu

R. Lockwood
Department of Geology, The College of William and Mary, Williamsburg, VA, USA
e-mail: rxlock@wm.edu

A. N. Grant
School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff, AZ, USA
e-mail: angrant@email.wm.edu

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1 Introduction

The Eastern Oyster (*Crassostrea virginica*) plays a vital role in the ecosystem of the Chesapeake Bay and Mid-Atlantic regions (Mann et al. 2009a). Oysters are ecosystem engineers that build habitat for fish and other invertebrate species, boost water quality by filtering bacteria and contaminants, and represent an important component of the food web (Haven and Morales-Alamo 1970; Meyer and Townsend 2000; Cressmann et al. 2003; Hoellein et al. 2015). Historically, oyster harvests have provided a key economic resource for the region (Paolisso and Dery 2010; Rick and Lockwood 2013).

The Pleistocene record provides evidence of widespread, thriving oyster reefs predating human settlement in the region, during the formation of the proto-Chesapeake Bay (Hargis and Haven 1995; USGS 1998; Reshetiloff 2004; Rick and Lockwood 2013). The earliest record of human harvest of Mid-Atlantic oysters dates back to the Late Archaic (ca 2500–2000 cal yr. BC) in the form of oyster middens, or archaeological deposits of kitchen waste material (Waselkov 1982; Custer 1989; Thompson and Worth 2011). Native American harvesting occurred for thousands of years, across the bay region, and is assumed to have involved harvesting of small clusters of shells from easily accessible reefs (Rick et al. 2014, 2016).

European settlement of the region began with the Jamestown Colony, which was established along the James River (Virginia) in 1607 (Rountree et al. 2007; Horn 2008). English settlers relied heavily on oysters as a food source, leaving a record of oyster harvesting in the form of dozens of shells recovered from an abandoned well within the settlement (Kelso 2004; Harding et al. 2008, 2010a). Although oyster harvesting has been a key component of the regional economy for thousands of years, these harvests have declined massively over the last 150–200 years and now represent a mere 1% of peak productivity (Rothschild et al. 1994; Harding et al. 2008; Beck et al. 2011; Wilberg et al. 2011).

By the late 1800s, harvest by industrial dredging caused a massive reduction in reef height through the removal of shell material faster than living oysters could replenish it (Hargis and Haven 1999). Natural oyster reefs have effectively disappeared in the modern bay, due to overfishing, disease, increased sediment input, and habitat destruction, leaving oyster populations depleted and in need of serious mitigation efforts (Rothschild et al. 1994; Mann and Powell 2007).

Oyster populations in the region have also been impacted by two prevalent parasitic diseases that increase oyster mortality rates (Carnegie and Burreson 2009). Dermo disease is caused by the parasite *Perkinsus marinus*, is prevalent in intermediate salinity (12–15 ppt) warmer waters, and was first documented in the Chesapeake Bay in 1949 (Andrews 1996; Burreson and Ragone Calvo 1996; CTDOAG 2016a). MSX (Multinucleated Sphere Unknown) is caused by the spore-forming protozoan *Haplosporidium nelsoni*, prefers more saline conditions (>15 ppt) and was first documented in the Mid-Atlantic region in 1957 (CTDOAG 2016b) as a result of the intentional introduction of the Japanese oyster (*Crassostrea gigas*) to Delaware Bay (Andrews and Wood 1967). Increased sediment influx from land clearance has further complicated the situation by hastening habitat destruction in areas of optimal oyster growth (Hargis and Haven 1999).

Early management approaches to Mid-Atlantic oysters focused on helping the fishery recover from natural and anthropogenic problems primarily for the benefit of the local economy. These approaches included the genetic enhancement of broodstock, the release of spat raised through aquaculture, and planting of dead shell (cultch) to act as substrate for settlement (Bartol and Mann 1997, 1999a, 1999b; Mann and Evans 1998; Southworth and Mann 1998; Wesson et al. 1999; Luckenbach et al. 1999; Mann 2000; Southworth et al. 2000). More recent efforts have embraced a broader strategy, prioritizing the mitigation of ecosystem services via protected areas, reduction of harvesting, and large-scale three-dimensional reef restoration (Luckenbach et al. 2005, Coen et al. 2006, 2007; North et al. 2010; Beck et al. 2011; Grabowski et al. 2012).

Pleistocene fossil reefs may provide insight into how oyster ecosystems functioned before human intervention in the Mid-Atlantic U.S. Although natural oyster reefs have dwindled to extinction in the modern Chesapeake Bay, Pleistocene oysters can yield information on shell size and growth rates that may prove vital for mitigation efforts. The goal of this study is to quantify oyster size and growth rates in the Mid-Atlantic region, across three timescales—Pleistocene, colonial, and modern—to assess the implications of this conservation paleobiological approach for oyster mitigation.

2 Methods

Pleistocene Localities

Samples of Pleistocene oysters were examined from the Virginia Museum of Natural History (VMNH) and field collections across five localities, distributed from southern Maryland to North Carolina (Fig. 1; Table 1). The northernmost of the Chesapeake Bay sites, Wailes Bluff (WB), is located at the mouth of the Potomac River in St. Mary's County, Maryland. This site, which has since been covered by a seawall, yielded molluscan material collected by L. W. Ward in 1971 (VMNH 71LW93). Bulk samples were collected from *C. virginica* shell layers distributed in a sandy silt matrix, thought to represent the late Pleistocene Tabb Formation (Fig. 2; Thompson 1972; Belknap 1979; Cronin 1979; Wehmiller and Belknap 1982; Rader and Evans 1993). Many of the molluscan species identified at Wailes Bluff are now

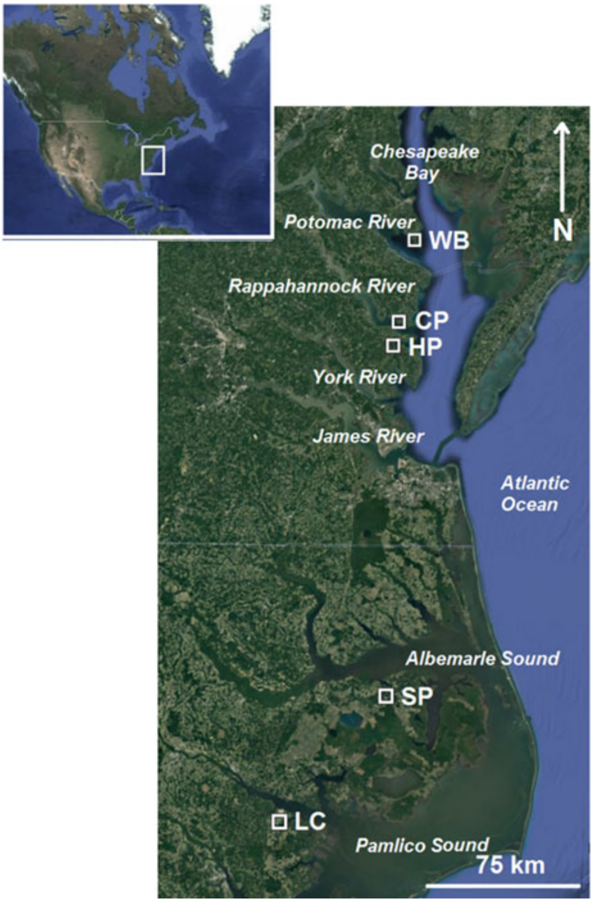

Fig. 1 Map of five localities in Maryland, Virginia, and North Carolina, from which Pleistocene fossil oysters were sampled (*WB* Wailes Bluff, *CP* Cherry Point, *HP* Holland Point, *SP* Stetson Pit, *LC* Lee Creek)

restricted to more southerly latitudes, suggesting a paleotemperature warmer than today (Blake 1953). Several brackish water taxa have been documented at this site, supporting a paleosalinity of approximately 15–30 ppt (Blake 1953; Cronin 1979).

Cherry Point (CP, also known as Norris Bridge) is a middle Pleistocene site located in Lancaster County, Virginia, near the mouth of the Rappahannock River (Fig. 1; Table 1). Although the site is no longer available for collecting due to development, B. W. Blackwelder and T. M. Cronin collected oyster specimens in 1978 (VMNH 78BB79A, B; VMNH T8TC56) from a fossiliferous sandy silt unit thought to represent the Shirley Formation (Fig. 2; Mirecki 1990; Mirecki et al. 1995). Ostracode assemblages at this site indicate a Pleistocene bottom temperature between 12.5 and 15 °C during winter and 27.5 °C during summer months (Cronin 1979), both of which are warmer than modern conditions at the site by at least 1–2 °C (Massmann et al. 1952). Paleosalinity is thought to have ranged between open sound (15–35 ppt) and estuarine (2–15 ppt) conditions (Cronin 1979).

Table 1 Location, stratigraphic unit, and geologic age of the five localities sampled for Pleistocene oysters

	State	Sample size (≥35 mm)	Latitude/longitude	Stratigraphic unit	Pleistocene interval
Wailes Bluff (WB)	MD	36 (36)	38.065560/76.365280°	Tabb	Late
Cherry Point (CP)	VA	36 (36)	37.634184/76.412830°	Shirley	Mid
Holland Point (HP)	VA	865 (611)	37.512088/76.432121°	Shirley	Mid
Stetson Pit (SP)	NC	225 (225)	35.866291/76.293768°	Undetermined	Late
Upper Lee Creek (ULC)	NC	85 (85)	35.324287/76.800213°	James City	Early
Lower Lee Creek (LLC)	NC	21 (21)	35.324287/76.800213°	Flanner Beach	Mid

The Lee Creek locality is divided into two sections: Upper Lee Creek (ULC) and Lower Lee Creek (LLC), respectively

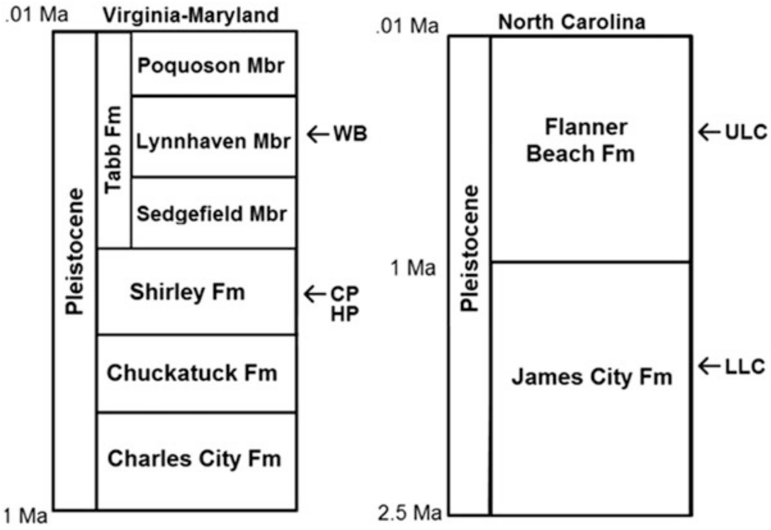

Fig. 2 Stratigraphic framework for four of the Pleistocene localities (*WB* Wailes Bluff, *HP* Holland Point, *CP* Cherry Point, *ULC* Upper Lee Creek, *LLC* Lower Lee Creek). The stratigraphic unit for Stetson Pit (SP) is undetermined

Holland Point (HP), the southernmost of the Chesapeake Bay sites, is located on the Piankatank River (Fig. 1; Table 1). Amino acid racemization dating of *C. virginica* and *Mercenaria* specimens suggests an age of approximately 195–243Ka (MIS 7 or 9, J. Wehmiller, personal communication 2016). The unit in which the oyster deposit occurs is thought to represent the Shirley Formation, which is middle Pleistocene in age (Fig. 2; C. R. Berquist, personal communication 2016). The exposed oyster deposit at Holland Point is laterally extensive (up to 25 m) and thick (up to 3 m), containing thousands of oysters, many of which are articulated and preserved in life position within a fine sandy, clayey silt matrix. Reconstructions of both paleotemperature and salinity were accomplished as part of the current study.

The northernmost site in North Carolina is Stetson Pit (SP, Fig. 1, Table 1), located at the mouth of the Albemarle Sound in Dare County, North Carolina, and subsequently covered by landfill material. Bulk samples, collected in 1979 by B. W. Blackwelder (VMNH 79BB32(D)), yielded several *C. virginica*. This shelly, sandy mud unit that was sampled has never been attributed definitively to a specific stratigraphic unit (Miller 1982), but its position above a U-series-dated coral suggests that it is late Pleistocene (late MIS 5a, J. Wehmiller personal communication 2016) in age. Using assemblages of temperature-sensitive ostracodes, York et al. (1989) identified a high proportion of cryptophilic species, suggesting relatively cooler temperatures compared to present-day Cape Hatteras, North Carolina. These ostracode assemblages, and the presence of molluscan taxa including *Rangia cuneata*, indicate a brackish paleosalinity (York et al. 1989).

The final site, Lee Creek (PCSD Phosphate Mine), is located on the Pamlico River in Beaufort County, North Carolina. The site was sampled by L. W. Ward in 1972 (VMNH 72LW8C, 72LW1B) and 1992 (VMNH 92LW60a) although it is currently inaccessible (Fig. 1; Table 1). This site produced *C. virginica* specimens at two stratigraphic horizons: Lower Lee Creek (LLC) within the James City Formation (early Pleistocene) and Upper Lee Creek (ULC) within the Flanner Beach Formation (middle Pleistocene) (Fig. 2; (Ward and Blackwelder 1987; Ward and Bohaska 2008). The James City beds yielded a variety of mollusks in a fossiliferous, medium-coarse grained quartz sand. Rare records of freshwater (i.e., *Corbicula*) and brackish (i.e., *Rangia*) taxa suggest that these beds represent an offshore barrier bar influenced by migrating channels that intermittently opened and closed, with more open-marine salinity conditions behind the back barrier (Ward and Blackwelder 1987; Ward and Bohaska 2008). The Flanner Beach sediments are characterized by a very fine sandy silt (Ward and Bohaska 2008), reflecting a back barrier muddy estuary with corresponding brackish paleosalinity (Ward and Bohaska 2008).

Field and Museum Sampling

Of the five sites studied, Holland Point is the only one still accessible for field sampling. We sampled the exposed oyster deposit at Holland Point in July 2011, in addition to describing the sedimentology and measuring the stratigraphic section. Samples were collected in five columns spaced approximately 3 m apart along the lateral extent of the deposit. We collected three bulk samples (spaced evenly apart according to deposit thickness) from each column ($n = 15$ samples total), using a 0.5 m^2 quadrat (Fig. 3).

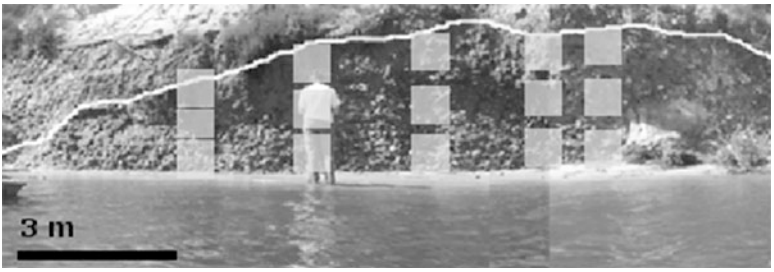

Fig. 3 Sampling transects of the oyster deposit at Holland Point. Samples were collected in five columns spaced approximately 3 m apart along the lateral extent of the deposit. Three bulk samples (spaced evenly apart according to deposit thickness) were collected from each column ($n = 15$ samples total), using a 0.5 m^2 quadrat

Bulk samples of *C. virginica* from the Virginia Museum of Natural History in Martinsville, Virginia, were examined from Wailes Bluff (VMNH 71LW93), Cherry Point (VMNH 78BB79A, B; 78TC56), Stetson Pit (VMNH 79BB32), and Lee Creek (VMNH 72LW1B, 72LW8C, 92LW60A).

Oyster Size and Abundance Data

Samples from Holland Point were sieved using a 4 mm mesh size, sorted, and molluscan whole specimens and hinge fragments were identified to the lowest taxonomic level possible (Abbott 1974; Spencer and Campbell 1987).

For each museum and field sample, we used digital calipers to measure shell height for all whole left valves of *C. virginica.* Shell height was measured as the distance from the umbo to the ventral-most edge of the shell. Although this distance is commonly referred to as “shell length,” it is more accurate to use the term “shell height” (Galtsoff 1964). The field site at Holland Point yielded 865 whole left valves of *C. virginica* for measurement. The number of museum specimens available for each Pleistocene site varied from 21 to 225 whole left valves.

A subset of these left valves was randomly selected to be sawed in half, using a diamond-tipped tile saw. The resulting bisected hinges were used to count shell bands in cross-section. We recorded the number of thick, dark gray shell bands that were continuous from the hinge to the outer shell layer (Fig. 4), to provide a proxy for biological age (e.g., life span) of each specimen, following Harding and Mann (2006) and Zimmt et al. 2016).

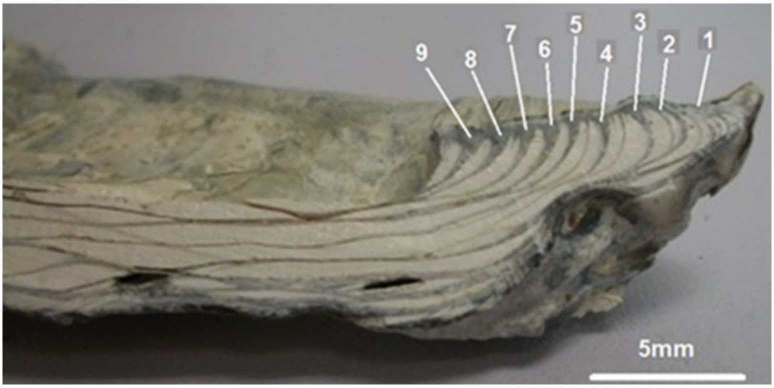

Fig. 4 Cross-section of bisected hinge from Holland Point, showing gray and white growth lines; *1–9* represent thick, gray shell bands that were continuous from the hinge to the outer shell layer and were counted to provide an approximate biological age (i.e., life span) for oyster specimens

Reconstructing Paleotemperature and Salinity

In order to standardize for paleoenvironment, we compiled information on paleosalinity and paleotemperature for each Pleistocene locality, except for Holland Point, from the literature.

To estimate paleosalinity at Holland Point, the raw abundance of all other molluscan specimens identified to the species level was assessed. For bivalves, whole shells and hinge fragments were sorted into left versus right valves and the larger of the two values was used to represent raw abundance for each sample. For gastropods, whole and fragmented specimens were sorted into apertures and apices and the larger of the two values was used to represent abundance for each sample. We compiled modern salinity tolerance ranges from the literature for those species with more than one occurrence at Holland Point (Federighi 1931; Andrews 1953; Menzel et al. 1966; Castagna and Chanley 1973; Buroker 1983; Zimmerman and Pechenik 1991; Grabe et al. 1993; Griffin 2001; Hill 2004, Zachary and Haven 2004; Wilson et al. 2005; Harding et al. 2010b; Cohen 2011).

To assess paleotemperature at Holland Point, one specimen of *C. virginica* was assessed using clumped isotope analysis by G. A. Henkes (Johns Hopkins University). A sub-sample of shell material was collected from the hinge area using a low-speed Dremel drill and analyzed following the methods of Henkes et al. (2013).

Additionally, two articulated *C. virginica* and one articulated *M. mercenaria,* all preserved in life position from Holland Point, were assessed for paleotemperature using sclerochronology under the supervision of G.S. Herbert (University of South Florida). Sub-samples (one sample per every 0.78–1.75 mm) were collected from each annual growth band of sectioned valves using a Dremel drill. Powdered material was dissolved in 100% H_3PO_4 at 25 °C for 24 h. The resulting CO_2 was separated, focused, and analyzed on a Thermo Finnigan Delta V Advantage IRMS in continuous flow mode coupled to a Gasbench II preparation device (Harke et al. 2015). Growing season paleotemperatures were calculated using the Craig (1965) calcite-water equation for *C. virginica* and the Grossman and Ku (1981) aragonite-water equation for *M. mercenaria*. The salinity range estimated from HP molluscan occurrences was used to determine $\delta^{18}O_{seawater}$ for these equations.

Modern and Colonial Data

Reconstructions of paleosalinity from the Pleistocene sites were used to identify modern and colonial sites with *C. virginica* living in similar salinity conditions. Data on shell height and growth rates in colonial and modern oysters were compiled from the published literature and management agencies as described below.

In Maryland, colonial data on mean shell height and growth rates were compiled from Miller (1986) and Catts et al. (1998) for four sites from similar salinity regimes (15–25 ppt), including St. Mary's City (sample size not published) and Ashcomb's Quarter ($n = 99$ shells). Data on modern shell height and growth rates were provided by M. Tarnowski (Maryland Department of Natural Resources) for six sites ($n = 1176$ shells) from Pocomoke and Tangier Sounds (15–25 ppt salinity zone) sampled from 2013 to 2015.

In Virginia, colonial data on shell heights and growth rates were acquired from Harding et al. (2008, 2010a) from the Jamestown Colony ($n = 363$ shells, salinity 15–30 ppt). Modern shell height and growth rate data were also compiled from published sources (Harding et al. 2008; Sisson et al. 2011) for eight sites ($n = 6916$ shells) in the James River (collected from 2006 to 2008) and Lynnhaven River (collected from 2005 to 2008), from the same salinity range.

We were unable to locate any colonial aged oyster data from North Carolina. Data on shell height and growth rates for modern North Carolina oysters were obtained from Puckett and Eggleston (2012), for six sites sampled from 2006 to 2008 ($n = 5443$ shells) in Pamlico Sound (15–30 ppt salinity zone).

3 Results

Paleoenvironmental Reconstruction of Holland Point

Paleotemperature

Clumped isotopic analysis of a single *C. virginica* valve from the Holland Point fossil deposit produced a $\delta^{13}C_{carb}$ composition of 0.47 ± 0.02‰PDB, $\delta^{18}O_{carb}$ of 2.08 ± 0.01‰PDB, and Δ_{47carb} of 0.725 ± 0.014‰ (Ghosh)(Ghosh et al. 2006; Huntington et al. 2009). This Δ_{47} value corresponds to an oyster growth temperature (i.e., averaged temperature at which the oyster was growing at this particular site, at this particular time) of 14.1 ± 5 °C. Given this paleotemperature and measured oxygen isotope value, solving the Kim et al. (2007) equilibrium oxygen isotope fractionation equation provides a $\delta^{18}O_{water}$ value of -3.44‰ SMOW.

Isotopic sclerochronological analysis of one *M. mercenaria* and two *C. virginica* shells from Holland Point yielded comparable results of $\delta^{18}O_{water} = -3.40$‰

SMOW. Using the Craig (1965) and Grossman and Ku (1981) equations, respectively, growing season paleotemperatures ranged from 5.3 to 20.5 °C for *C. virginica* and 10.9 to 20.9 °C for *M. mercenaria*. This growth temperature is cooler than the modern Piankatank River, which routinely reaches temperatures between 25 and 30 °C during the summer growing months of modern *C. virginica* (Harding et al. 2010b). Sclerochronological analyses of other species would be required to determine whether *C. virginica* stopped growing in either the summer or winter months at this site in the middle Pleistocene.

Paleosalinity

Almost 1500 whole and fragmented shells, representing 21 macroinvertebrate species other than *C. virginica*, were identified in the bulk samples collected from the Holland Point deposit. Raw abundance of these species ranged from 1 to 515 (mean = 55.62) per sample. Six taxa were excluded from the salinity analyses because they could not be identified to the species level (undetermined crab, sponge (likely *Cliona*), barnacle (likely *Balanus*)) or because data on salinity tolerance of the modern representatives were not readily available (*Trittia trivittata, Crepidula convexa,* and *Melanella polita*). When rare taxa, those with only a single occurrence, are excluded, a paleosalinity range of 16–32 ppt encompasses all remaining species (Fig. 5). This salinity is higher than that of the modern Piankatank River, which fluctuates between 6 and 23 ppt (Harding et al. 2010b).

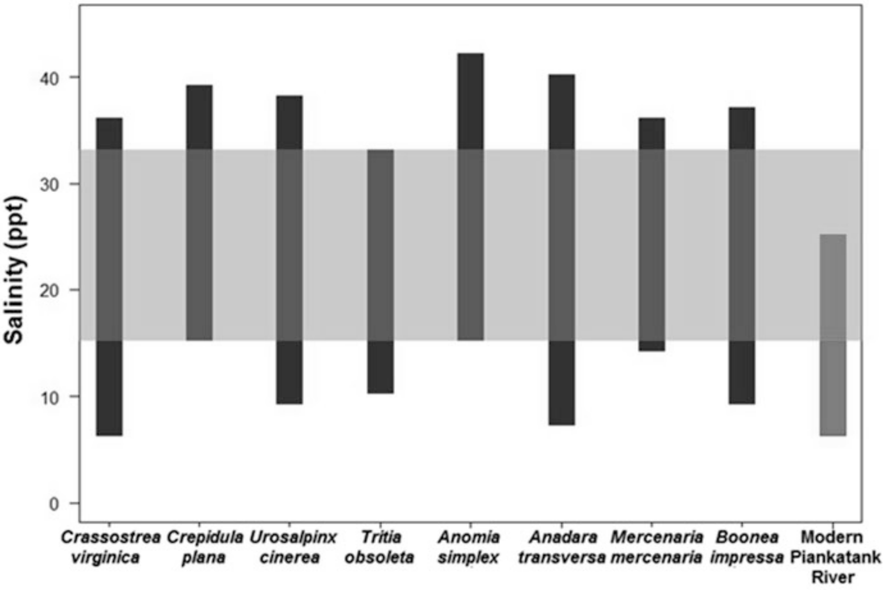

Fig. 5 Modern salinity tolerances of fossil macroinvertebrate species with abundance greater than 1 recorded at Holland Point (Virginia); shaded region (15–32 ppt) encompasses salinity range within which all taxa could co-occur

Shell Height

Shell height was compared across all of the Pleistocene, colonial, and modern localities using size frequency distributions and non-parametric statistical tests. We excluded specimens ≤ 35 mm in shell height in order to avoid sampling spat (Mann et al. 2009a). Kolmogorov-Smirnov tests for normality indicated that the shell height data were non-normally distributed for most fossil ($KS_{21\text{–}655} = 0.08$–$0.22$, $p = 0.20$–0.0001) and modern ($KS_{24\text{–}5784} = 0.05$–$0.17$, $p = 0.20$–0.0001) samples. We therefore used a non-parametric test (Mann-Whitney U) to test for differences in mean shell height among Pleistocene, colonial, and modern oysters across three geographic regions: (1) upper Chesapeake Bay (Maryland), (2) lower Chesapeake Bay (Virginia), and (3) North Carolina.

Starting with the Maryland portion of the Chesapeake Bay, late Pleistocene oysters tend to be larger than colonial or modern oysters from similar salinity regimes (15–25 ppt, Fig. 6, Table 2). Pleistocene oysters also exhibit more strongly right-skewed size frequency distributions than modern oysters (Fig. 6).

Moving south, into the Virginia portion of the bay, middle Pleistocene (MP) oysters were statistically significantly larger than both colonial and modern oysters from similar salinity regimes (15–30 ppt, Fig. 7, Table 2). Pleistocene oysters reached a maximum size of nearly 260 mm, in comparison to colonial (124 mm) and modern (148 mm) specimens. The right tails of the size frequency distributions for both the modern and colonial oysters appear truncated. These distributions are missing the larger adults that contribute to the strongly right-skewed distribution of the Pleistocene sample (Fig. 7).

In Albemarle and Pamlico Sounds in North Carolina, MP and LP oysters show no significant difference in size or the shape of the size frequency distribution from modern oysters from similar salinity regimes (15–30 ppt, Fig. 8, Table 2).

Growth Rate

Growth rates were plotted for Pleistocene, colonial, and modern oysters by plotting biological age (i.e., life span) of each specimen versus shell height (Figs. 9 and 10). We excluded specimens ≤ 35 mm in shell height in order to avoid sampling spat (Mann et al. 2009a). We calculated the slopes of these growth trajectories (i.e., growth rates) and compared them using an analysis of covariance (ANCOVA, modelled as linear). Growth rates were compared among Pleistocene, colonial, and modern oysters across three geographic regions: (1) upper Chesapeake Bay (Maryland), (2) lower Chesapeake Bay (Virginia), and (3) North Carolina.

In the upper Chesapeake Bay, growth trajectories in Pleistocene oysters extend beyond 12 years (Fig. 9). In contrast, growth trajectories for colonial and modern oysters rarely extend beyond 5 years (Fig. 9). Using ANCOVA to compare growth rates in Maryland oysters between 0 and 5 years of age suggests that modern oysters are growing significantly faster than Pleistocene or colonial oysters from similar salinity regimes (15–30 ppt, Fig. 9, Table 3). Whereas modern oysters record

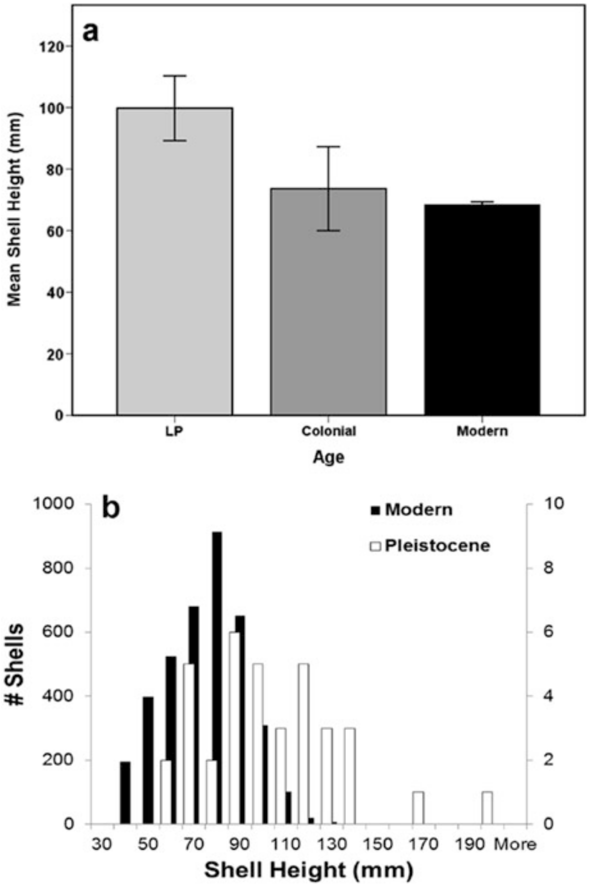

Fig. 6 Shell height (mm) trends in late Pleistocene (LP), colonial and modern oysters from sites in the upper Chesapeake Bay region (Maryland) with salinities ranging from 15 to 25 ppt. (**a**) Mean shell height ± S.E.; (**b**) Size frequency distributions for Pleistocene and modern oysters

Table 2 Mann-Whitney U tests comparing shell height (mm) in Pleistocene, colonial, and modern oysters from Maryland, Virginia, and North Carolina

	Maryland	Virginia	North Carolina
MP vs. LP	–	–	**$Z_{225,21} = -2.93$, $p = 0.003$**
MP vs. colonial	–	**$Z_{647,364} = -4.48, p < 0.0001$**	–
MP vs. modern	–	**$Z_{647,6916} = -15.15$, $p < 0.0001$**	$Z_{21,5443} = -1.05$, $p < 0.29$
LP vs. colonial	$Z_{36,3} = -1.69$, $p = 0.09$	–	–
LP vs. modern	**$Z_{36,1176} = -6.44$, $p < 0.0001$**	–	**$Z_{225,5443} = -3.76$, $p < 0.0001$**
Colonial vs. modern	$Z_{3,1176} = -0.69$, $p = 0.49$	**$Z_{364,6916} = -9.56, p < 0.0001$**	

Statistically significant differences ($p \leq 0.05$) highlighted in bold; all oyster comparisons from similar salinity regimes; *MP* middle Pleistocene, *LP* late Pleistocene

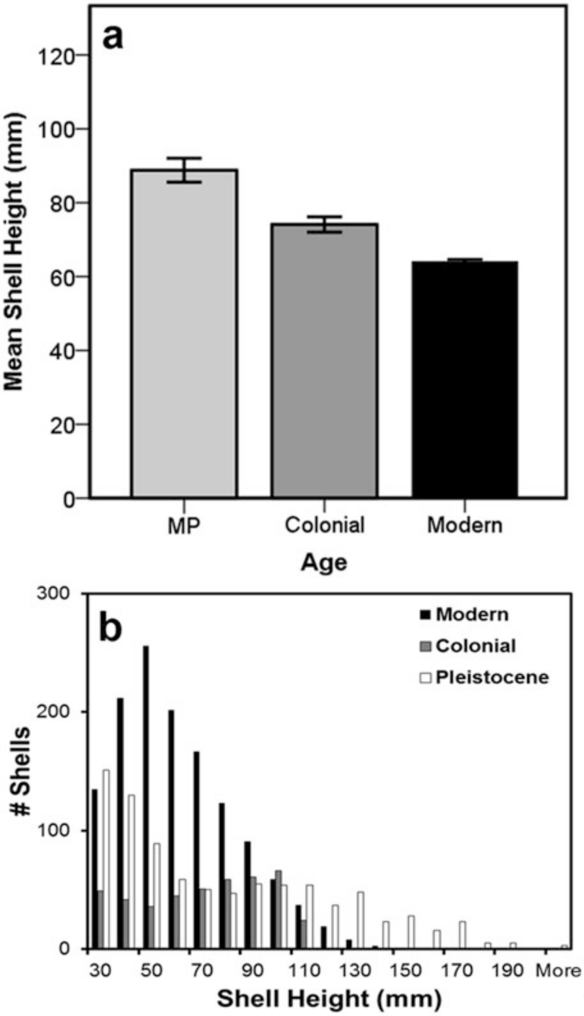

Fig. 7 Shell height (mm) trends in middle Pleistocene (MP), colonial, and modern oysters from sites in the lower Chesapeake Bay region (Virginia) with salinities ranging from 15 to 30 ppt; (**a**) Mean shell height ± S.E.; (**b**) Size frequency distributions for Pleistocene (MP), colonial, and modern oysters

average growth rates of 14 mm/year (slope), colonial (slope = 11.78 mm/year), and Pleistocene oysters grow significantly more slowly (slope = 8.51 mm/year).

Comparisons of growth trajectories among Pleistocene, colonial, and modern oysters in the lower Chesapeake Bay yield similar results. Growth trajectories in Pleistocene oysters extend beyond 20 years, while colonial and modern oysters rarely live longer than 5 years (Fig. 10). Mean biological age (i.e., life span, *x* axis of Fig. 10) ranges from 8.6 years at the Holland Point fossil locality to 2.38 years at the Jamestown colonial site to 2.59 years in modern bay sites with salinities ranging from 15 to 30 ppt. Comparison of growth rates in Virginia via ANCOVA (oysters aged 0–5 years) reveals that Pleistocene oysters have slower growth rates than either colonial or modern oysters from similar salinity regimes

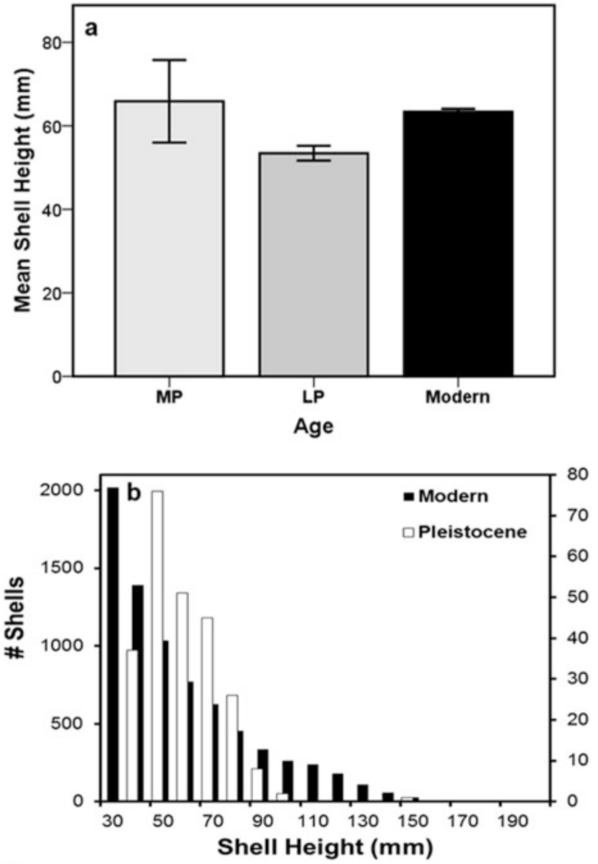

Fig. 8 Shell height (mm) trends in middle Pleistocene (MP), late Pleistocene (LP), and modern oysters from North Carolina with salinities ranging from 15 to 30 ppt; (**a**) Mean shell height ± S.E.; (**b**) Size frequency distributions for Pleistocene (MP and LP combined) and modern oysters

(15–30 ppt, Fig. 10, Table 3). Colonial (slope = 28.94 mm/year) and modern oysters (slope = 19.73 mm/year) both have significantly greater growth rates than Pleistocene (slope = 8.24 mm/year) oysters.

Interestingly, growth trajectories in North Carolina oysters do not extend beyond 4 years of age, for either Pleistocene or modern oysters. ANCOVA reveals that growth rates in oysters $\leq$ 5 years are significantly steeper in modern, in comparison to Pleistocene oysters, when salinity is controlled for (15–30 ppt, Fig. 11, Table 3). The slope of modern oysters (23.77 mm/year) is almost three times that of Pleistocene oysters (8.87 mm/year).

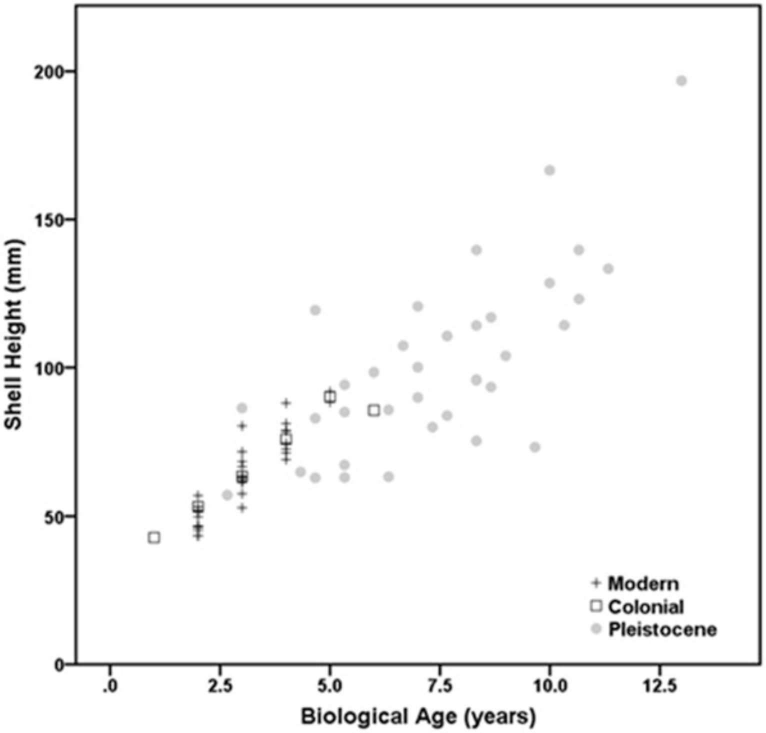

Fig. 9 Growth rate trends in Pleistocene and modern oysters from sites in the upper Chesapeake Bay region (Maryland) with salinities ranging from 15 to 30 ppt

Table 3 Results for ANCOVA comparing growth rates (shell height (mm) vs. biological age (years)) in Pleistocene, colonial, and modern oysters from Maryland, Virginia, and North Carolina

	Maryland	Virginia	North Carolina
Pleistocene vs. colonial	$F_{2,11} = 3.64, p = 0.08$ Not significant	**$F_{2,33} = 9.93, p < 0001$** **Colonial > Pleistocene**	–
Pleistocene vs. modern	**$F_{3.43} = 29.52,$** **$p < 0001$** **Modern > Pleistocene**	**$F_{2,1067} = 570, p < 0001$** **Modern > Pleistocene**	**$F_{2,875} = 472.53,$** **$p < 0001$** **Modern > Pleistocene**
Colonial vs. modern	**$F_{2.37} = 104.18,$** **$p < 0001$** **Modern > Pleistocene**	**$F_{2,1057} = 571.02,$** **$p < 0001$** **Modern > Colonial**	–

Growth rates modelled as linear for oysters $\leq$5 years; statistically significant differences ($p \leq 0.05$) highlighted in bold, all comparisons are controlled for salinity regime

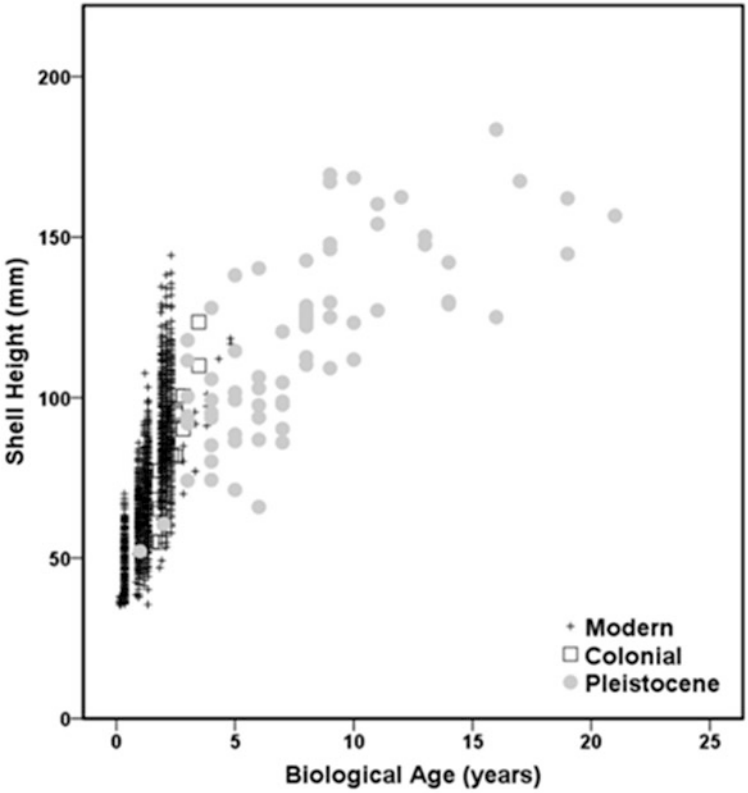

Fig. 10 Growth rate trends in Pleistocene (middle and late Pleistocene combined), colonial, and modern oysters from sites in the lower Chesapeake Bay region (Virginia) with salinities ranging from 15 to 30 ppt

4 Discussion

Comparing Pleistocene to Modern Oysters

Fossil oysters from the Chesapeake Bay are 1.3–1.6 times larger than oysters from either colonial or modern times (depending on location). This difference is not the result of slower growth rates. In fact, colonial and modern oysters grew approximately 3–4 times faster than Pleistocene oysters in the bay, even when growth rates are only calculated for younger, faster-growing individuals (0–5 years). The size difference is driven by the presence of significantly longer-lived (up to 3.6 times longer) adults in the Pleistocene assemblages. Growth trajectories in fossil Chesapeake Bay oysters continued beyond 5 years of age (Figs. 9 and 10), but colonial and modern bay populations rarely lived that long.

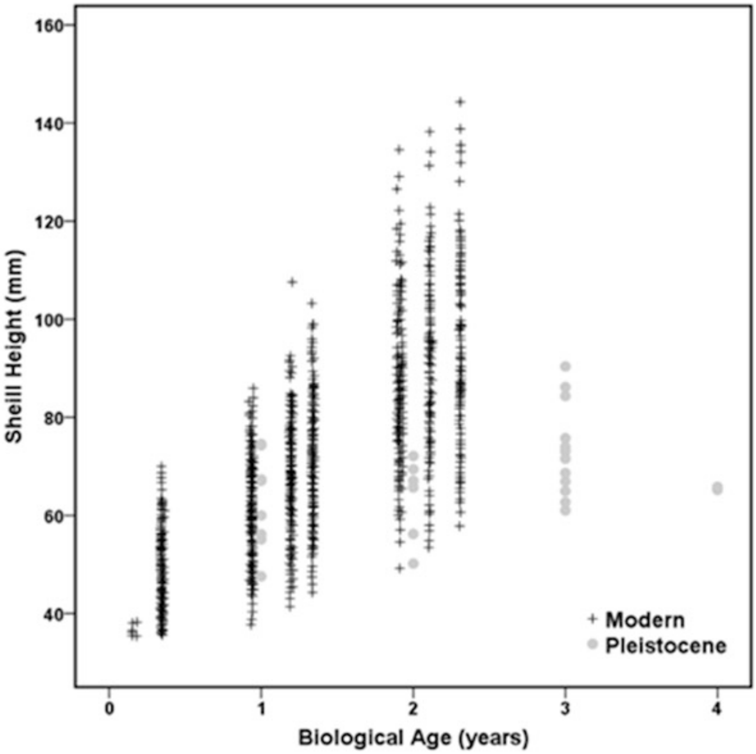

Fig. 11 Growth rate trends in Pleistocene (middle and late Pleistocene combined) and modern oysters from sites in the Pamlico Sound region of North Carolina with salinities ranging from 15 to 30 ppt

The same pattern does not hold for North Carolina. While there is no significant difference in size between middle Pleistocene and modern oysters, late Pleistocene oysters are significantly smaller than modern ones. Although growth rates in modern oysters in Pamlico Sound are 6–7 times faster than fossil oysters, the short life spans of both fossil and modern oysters result in little to no difference in these population parameters through time.

Environmental Controls on Oyster Size

A number of factors could be responsible for this significant decrease in oyster size in the Chesapeake Bay from the Pleistocene to the modern. Sampling, for both modern and fossil localities, was accomplished via bulk sampling, either by hand (Pleistocene) or with the use of hydraulic patent tongs (modern). The open dimensions of patent tongs make it possible to sample all of the oysters inhabiting one square meter of bay bottom. Both sampling techniques are therefore random with respect to size, suggesting that sampling bias is unlikely to be affecting these trends.

The likelihood of fossil preservation varies according to shell size and thickness, such that smaller mollusks are, in general, less likely to be preserved than larger ones, due to processes such as fragmentation and dissolution (Cummins et al. 1987; see reviews in Martin 1999; Kidwell 2013). In the field, these Pleistocene sites are extremely well-preserved and qualitative inspection of the oyster shells reveals little taphonomic damage (including few signs of dissolution or corrosion). The majority of oysters at Holland Point and Stetson Pit (Miller 1982) were still articulated and oriented in life position and the clayey-silty matrix shows no evidence of the molds and casts that would be expected under dissolution regimes. The bimineralic and relatively thick shell of oysters also makes it less likely that they would have experienced dissolution, especially given the preservation of aragonitic material at the same localities.

Environmental factors, including salinity, temperature, and nutrients, are closely tied to oyster size in modern settings. Although oysters are tolerant of a wide range of salinity conditions (0–40 ppt; Quast et al. 1988; Shumway 1996), optimal growth and reproduction occur between 10 and 28 ppt, with larval recruitment only possible above 6 ppt (Wilson et al. 2005). Salinity is generally negatively correlated to oyster size in the modern Chesapeake Bay, not because of a direct link between salinity and oyster size, but because of the high occurrence of disease, predators, and boring sponges in fully marine conditions (Galtsoff 1964; Paynter and Burreson 1991; VOSARA 2016). By explicitly limiting modern comparisons to those with similar salinity regimes, we have controlled for the complicating effects of salinity on these data.

Growth studies in the Chesapeake Bay found that modern *Crassostrea virginica* grow between July and October, with growth stopping when mean temperatures dropped below 10 °C (Paynter and Dimichele 1990). Though environmental conditions are similar during some spring months, the oysters exhibit no growth during these periods (Paynter and Dimichele 1990). The Pleistocene sites sampled in this study all represent interglacial intervals. Bottom water temperatures at these sites in the Pleistocene range from substantially warmer (+10 °C at Cherry Point, Virginia) to substantially colder (−10 °C at Holland Point, Virginia) than the same locations today (NDBC 2016). The colder paleotemperatures for Holland Point (Virginia) are similar to those recorded today between Ocean City, Maryland and Lewes, Delaware (NOAA NCEI 2016). The warmer paleotemperatures documented at Cherry Point (Virginia) correspond to temperatures observed today near Wilmington, North Carolina. If the changes in shell height were driven by temperature, we would expect oysters from Pleistocene bay localities with warmer temperatures (i.e., Cherry Point and Wailes Bluff, Maryland) to differ from those from localities with cooler temperatures (i.e., Holland Point, Virginia). In reality, there is no significant difference in average or maximum shell height at these three localities.

Like most marine invertebrates, oysters grow larger under higher nutrient conditions (Berg and Newell 1986; Rice and Rheault 1996). Although the complex history of nutrient pollution in the Chesapeake Bay has been reconstructed in detail for the last millennium (Cooper and Brush 1991; Cooper 1995; Zimmerman and Canuel 2002; Kemp et al. 2005), considerably less is known about nutrients along the Mid-Atlantic Coastal Plain during the Pleistocene. Krantz (1990) sampled growth bands of middle Pliocene (Yorktown Formation) to early Pleistocene (James City Formation) scallops from Virginia and found evidence of seasonal increases in productivity (interpreted as spring phytoplankton blooms), but no record of upwelling. This result suggests that local nutrient levels were most likely lower in the Pleistocene than during historic and modern times. This increase in nutrients may be driving the increase in oyster growth rates observed in the historic and modern Chesapeake Bay (Kirby and Miller 2005; Harding et al. 2008; Mann et al. 2009b), but it cannot explain the smaller shell sizes and shorter longevities. Until proxy data for local productivity are available throughout the Pleistocene, it will be difficult to quantify the effects of primary productivity on oyster growth in the Mid-Atlantic region through time.

Human Factors Influencing Oyster Size

In addition to environmental factors, two anthropogenically driven factors are affecting historical and modern oyster sizes: disease and overharvesting. Two diseases, Dermo and MSX, exert a massive influence on oyster abundance in the bay today. Mortality is higher with MSX although the virulence of Dermo appears to have increased rapidly after the introduction of MSX (Burreson and Ragone Calvo 1996; Carnegie and Burreson 2009). Today, MSX is thought to kill the majority of oysters larger than 51 mm in high salinity regions of the bay. Disease-resistant strains of *C. virginica* exist (Brown et al. 2005; Encomio et al. 2005; Carnegie and Burreson 2011), but the majority of oyster growers prefer to grow triploid (non-reproductively active) oysters. These oysters, which have three sets of chromosomes, are just as susceptible to disease but tend to grow faster and reach market size before dying.

Studies of the sustainability of Native American and colonial harvesting are just beginning, but a compilation of oyster size across 28 archaeological sites spanning 3500 years of Native American harvest suggests that shell height remained relatively stable throughout this interval (Rick et al. 2016). Although Native Americans harvested oysters for thousands of years prior to European colonization, early English settlers reported massive oyster reefs covering the bay and its tributaries (Wharton 1957; Hargis and Haven 1999; Mann et al. 2009b; Rick et al. 2014).

Measures of Colonial Era oyster shell height and growth rates, using similar techniques to those used here, suggest that Jamestown Colony oysters were intermediate in size between Pleistocene and modern oysters (Harding et al. 2008, 2010a). Their growth rates were elevated, relative to both modern and Pleistocene growth rates (Harding et al. 2008). Kirby and Miller (2005) observed the same pattern in colonial oysters from the St. Mary's and Patuxent Rivers (Maryland) and argued that this pattern was the result of increased nutrient availability due to land clearance. By 1860, oyster growth rates began to decrease, with the initiation of harvesting by dredging, combined with hypoxia and harmful algal blooms (Kirby and Miller 2005).

Today, oyster size and population density are at historic lows, in part due to the culling of the larger tail of the size frequency distribution that is highlighted by comparisons between Pleistocene and modern oyster sizes. Like disease, harvesting disproportionately affects the larger, more reproductively active adult oysters (Hutchings and Reynolds 2004). In fact, the average mortality of these larger oysters exceeds 60% on natural oyster bars in the Piankatank (Harding et al. 2010b), James (Mann et al. 2009a), and Great Wicomico (Southworth et al. 2010) Rivers.

Implications for Restoration

This study has documented a substantial decrease in oyster shell size in the Chesapeake Bay from the Pleistocene to today. This difference in shell size is not due to a decrease in growth rates or culling of smaller oysters. Instead, it is driven by the culling of oysters at the larger end of the size frequency distribution in the modern bay, due to both overharvesting and disease. The elimination of large adults from the population is a common sign of overharvesting in many marine species (Hutchings and Reynolds 2004; Berkeley et al. 2004; Birkeland and Dayton 2005; Hsieh et al. 2006).

With that in mind, it is important to note that conservation efforts for Chesapeake Bay oysters focus almost exclusively on early life stages—in particular larvae and spat. These approaches include: (1) distribution of cultch on the bay floor to increase the likelihood of larval settlement, (2) rearing and release of oyster larvae, and (3) minimum size restriction on oysters harvested from both aquaculture (2 in.) and natural beds (3 in.)(Kennedy 1989; Mann and Powell 2007; Kennedy et al. 2011; Wilberg et al. 2011; Md. Code Regs. § 08.02.04.11; 4VA Admin Code 20-260-30). Millions of dollars are spent on these approaches each year (Luckenbach et al. 1999; Mann and Powell 2007; Beck et al. 2011; zu Ermgassen et al. 2012) but, from a statistical standpoint, very few of these oysters will actually settle and grow to market size.

Efforts devoted to preserving adult oysters are minimal by comparison. Only a small percentage of oyster habitat is protected from harvesting for the long term (= sanctuaries, 9–25% or 9000 acres in Maryland, <2% or 200 acres in Virginia; Schulte et al. 2009; MDDNR 2016; VMRC 2016a), which, in turn, protects both the early and late stage oysters growing there. The majority of protected areas in Virginia are closed to harvesting for only 1 to 3 years at a time (VMRC 2016a). This approach means that adult oysters are afforded little to no protection in the bay, despite the fact that they are the most reproductively important members of the population (Mann et al. 2009a, b). Because older oysters put exponentially more energy into reproduction and less into shell growth, lack of protection of adults has a catastrophic effect on oyster population growth. Similar patterns have been documented across a wide range of marine and freshwater fisheries (Berkeley et al. 2004; Birkeland and Dayton 2005; Hsieh et al. 2006; Venturelli et al. 2009; Arlinghaus et al. 2010). In the Chesapeake Bay, the overfishing of larger specimens and culturing of triploid specimens also means that disease resistance is evolving exceptionally slowly in oysters (Encomio et al. 2005). These problems are further compounded by the fact that oysters are sequential protandric hermaphrodites and that the ratio of females in a population increases with increasing age/size (Kennedy 1983; Heffernan et al. 1989; Harding et al. 2013). Oysters start their lives as male, and, in the Chesapeake Bay, do not transition to female until they are at least 60 mm long (approximately 1.6 years old; Harding et al. 2013). Thus, the culling of the larger sizes of oysters also preferentially removes females from the population.

The exception to preferential removal is areas of the bay that have historically avoided long-term harvesting because they are privately owned or excessively polluted. For example, larger, more disease-resistant oysters have been documented recently in locations such as Tangier Sound (Blankenship 1997; Encomio et al. 2005) and the Elizabeth River (Schulte et al. 2009; CBF 2016). This finding suggests that Chesapeake Bay oysters have the potential, if not the opportunity, to evolve disease resistance and grow to larger sizes that approach those seen in the Pleistocene record.

The Pleistocene record of Chesapeake Bay oysters emphasizes the significant extent to which colonial and modern populations have experienced age and size truncation. Management solutions to age truncation in marine fisheries include: (1) implementation of a maximum size or slot limit, (2) the establishment of marine protected areas (MPA), or (3) significant lowering of exploitation rates (Berkeley et al. 2004; Venturelli et al. 2009; Hixon et al. 2014). In many freshwater and some marine species, fishery size restrictions include both a maximum and minimum (slot limit), or a restriction based on reproductive stage. For example, management of the blue crab (*Callinectes sapidus*) in the Chesapeake Bay includes: (1) an MPA (Lipcius et al. 2003) and (2) fishing restrictions based on egg mass and molting stage, in addition to overall size (MDDNR 2016; VMRC 2016b). The reproductive stage of oysters would be difficult for waterpeople to determine because they are broadcast spawners (Kennedy 1983; Heffernan et al. 1989). Maximum size restrictions could, however, be enforced because minimum size restrictions are already in effect for oysters collected in the bay.

MPAs are areas of oceans or lakes that are protected from human activity to conserve natural or cultural resources. MPA approaches have proven useful across a wide variety of fishery species (Russ 2002; Halpern 2003; Pelletier et al. 2005), but effectiveness varies according to the size of the MPA and its duration (Claudet et al. 2008; Edgar et al. 2014). Harvest moratoria are controversial but have been suggested in the past by both ecological and economic managers to preserve oyster resources in the bay (Schulte et al. 2009; Kasperski and Wieland 2010; Wilberg et al. 2011).

If conservation funding were to shift toward protection of older, reproductively more active oysters, it would represent a more efficient approach, as each adult female produces an average of 2–115 million eggs per year, increasing with age (Brooks 1996). This approach is not without its challenges, especially given the importance of sustaining a culture supporting the local waterpeople (Paolisso 2007; Paolisso and Dery 2010). But the benefits of shifting funding priorities to preserving large, disease-resistant oysters make it worthwhile. The importance of prioritizing adult over early life stages has been recognized for several other aquatic species (Berkeley et al. 2004; Birkeland and Dayton 2005; Hsieh et al. 2006; Venturelli et al. 2009).

A Role for Conservation Paleobiology

Oysters from the Mid-Atlantic states represent an excellent example of how fossil data can inform conservation issues. Because humans have inhabited this region for at least 13,000 years (Dent 1995; Lowery et al. 2010), and harvests were not tracked until the 1870s (Lotze 2010; zu Ermgassen et al. 2012), a sizeable gap exists in our understanding of how these ecosystems have changed over long timescales. By the time marine scientists established monitoring of bay oysters in the 1940s, oyster populations were already decimated by 75 years of dredging (Haven et al. 1978; Rothschild et al. 1994; Rountree et al. 2007; zu Ermgassen et al. 2012). Given the effects of introduced disease and increased sediment influx, the oyster beds that we study today tell us very little about how healthy oyster reefs function, either in the past or present. One could argue that bay managers have never seen a healthy oyster reef.

Pleistocene fossil assemblages can serve as a baseline for Chesapeake Bay oyster mitigation. These assemblages allow us to quantify body size, growth rates, and other factors that can be used to shape modern mitigation efforts.

Combining historical (zu Ermgassen et al. 2012), archaeological (Rick and Lockwood 2013; Rick et al. 2016), and paleobiological (this volume) approaches makes it possible to bridge these timescales and to assess how oysters have responded to various pressures, including harvesting, climate, and sea level change in the past. Conservation paleobiology plays a particularly important role, as the only approach to yield information on ecosystems before human settlement. In the end, the fossil record provides us with a crucial baseline for mitigation, a glimpse into the world of Mid-Atlantic oysters before humans.

5 Conclusion

In conclusion, Pleistocene oysters from the Chesapeake Bay region are larger, and longer-lived than either colonial or modern oysters. This pattern is not the result of environmental shifts in salinity or temperature. Instead, it is driven by culling of the larger tail of the shell size frequency distribution in the modern bay, suggesting that both human harvesting and disease are eliminating the larger, reproductively more active female members of the population. Solutions to this size and age-skewed population structure include: (1) decreasing harvest pressure, (2) establishing a maximum size limit, and (3) designating MPAs specifically for oysters in the Chesapeake Bay. The conservation paleobiologic approach applied in this study emphasizes the impact that human activities have had on these ecosystem, at the same time providing a baseline for future mitigation.

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