

The effect of survivorship bias on archaeological oyster valve size metrics: implications for fisheries baselines



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ABSTRACT

Oysters (*Ostreidae*) are ecological and cultural keystone species that have been exploited by humans for millennia. Oyster size is a good proxy for population health, and researchers frequently use valve height and length measurements from archaeological and paleontological contexts that provide historical ecological baselines with potential to inform present-day management around the world. Oyster fragmentation in the archaeological record, however, is not commonly considered in studies of oyster size. This study presents the first systematic investigation of the effects of oyster fragmentation on eastern oyster (*Crassostrea virginica*) size metrics. Oyster assemblages including whole valves, valve fragments with hinges, and valve fragments lacking hinges were analyzed from stratified contexts at two Florida Gulf coast sites, Garden Patch (8DI4) and Calusa Island Midden (8LL45). Through comparisons of weight, height, length, and survival rates of whole valves, and the number and weight of fragmented valves, we show that survivorship bias—the selective preservation of whole valves of specific size ranges—explains significant variation in oyster valve size metrics. In some cases, survivorship bias is the primary driver of whole valve size differences between sampling units, indicating that whole valve samples are not representative of the pre-fragmented population. This conclusion has significant implications for current interpretations of archaeological oyster assemblage valve size as a proxy for past oyster reef health and effects of human predation and management. We suggest several methods for recognizing the confounding effects of survivorship bias in studies of archaeological oyster valve metrics and encourage continued critical evaluation of the archaeology of oyster and other shellfish assemblages and interrogation of their historical ecological implications in the present.

1. Introduction

Archaeologists have long been interested in understanding the effects of human harvest on shellfish populations around the world, including oysters (*Ostreidae*) (Rick, 2024; Thomas, 2015). A key metric for evaluating oyster and other shellfish population health through time is valve size, which is reflective of the animal's age in relation to ontogenetic growth rates and the microenvironmental conditions in which the individual lives (e.g., Bartol et al., 1999; Campbell, 2008). Accordingly, researchers frequently have used valve height and length measurements from archaeological, paleontological, and modern contexts to provide baselines for assessing environmental change and past human impacts that have potential to inform present-day management (e.g., Campbell, 2008; Lockwood and Mann, 2019; Rick et al., 2016; Robson et al., 2024). Archaeological shellfish assemblages are often highly fragmentary, however, with research on clams (Mactridae and Veneridae), mussels (Mytilidae), and other taxa emphasizing the need to account for fragmented specimens in size reconstructions (e.g., Campbell and Braje, 2015; Hillis et al., 2024; Singh and McKechnie, 2015).

In North America, several studies have analyzed archaeological, fossil, and modern eastern oyster (*Crassostrea virginica*) height and length through time, documenting patterns of size increase, decline, and stability, which vary at the site, watershed, and regional scale (see Hesterberg et al., 2020; Jenkins and Gallivan, 2020; Lockwood and Mann, 2019; Lulewicz et al., 2017; Rick et al., 2016; Thompson et al., 2020; Savarese et al., 2016). Such studies often rely on measurement data from whole left valves, sometimes including quantification of left valve hinge fragments, and these data are collected in both field settings during excavation and through select collection and curation of whole left valves in laboratory settings (Green et al., 2024).

While methods to account for fragmented valves through size reconstructions have been developed for some bivalve taxa, no such method currently exists for oysters because the relationship between valve features that preserve well (i.e., hinges) and overall shell size has so far proven inconsistent (e.g., Campbell, 2010:185). Consequently, studies of archaeological oyster size have proceeded with data from whole valves without adequately accounting for the effects of fragmentation. Moreover, it is rare in published studies of archaeological

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oyster valve size to analyze and report all valve fragments from excavated deposits, precluding an opportunity to investigate taphonomic relationships between all components of an oyster assemblage (e.g., whole valves and valve fragments with or without hinges; Fig. 1). Lack of attention to specimen fragmentation in the archaeological record and its effect on oyster valve size metrics obscures a potentially important source of variation and hinders comparisons of results and interpretations across assemblages.

Here, we present results of the first empirical study of taphonomic fragmentation effects on valve size metrics in eastern oyster archaeological assemblages that account for all represented oyster specimens. Exemplary of the many oyster-bearing archaeological coastlines around the world, the Gulf coast of Florida (southeastern U.S.A.) is renowned for Indigenous oyster middens and mounds representing millennia of oyster harvest and shell deposition (e.g., Pluckhahn et al., 2023; Sassaman et al., 2017; Saunders and Russo, 2011; Schwadron, 2017, Fig. 2). Through an unselective analysis and quantification of all eastern oyster whole valves and valve fragments from two Florida Gulf coast assemblages from the Calusa Island Midden (8LL45) and Garden Patch (8DI4) sites, we show that survivorship bias—the selective preservation of whole valves of specific size ranges—affects size representation in whole valve samples in significant ways. Our calculations indicate that survivorship bias is the primary driver of whole valve size differences between sampling units in some cases, indicating that whole valve samples are not representative of the pre-fragmented population. These results reveal the necessity of accounting for fragmentation effects in measurements of oyster size. We recommend ways of recognizing the confounding effects of survivorship bias and we encourage renewed efforts to develop regression formulae for estimating whole valve size from fragments, which will increase both the accuracy of valve size studies and their value for understanding fisheries baselines.

2. Background

Oysters (Family Ostreidae) are important bivalve mollusks found around the world, often forming reefs and clusters in bays, estuaries, and other calm water environments (Kennedy et al., 1996). In eastern North America, *Crassostrea virginica* Gmelin (eastern oyster) is found from the Gulf of Mexico through the Gulf of St. Lawrence and was an important food resource for Native Americans for thousands of years. *C. virginica* are often oval, but their growth is dictated by their surroundings and they can take on a wide variety of shapes. The two valves of *C. virginica* are asymmetrical, with one valve being cupped (referred to as the left valve) and the other being flat or slightly convex (right valve) and the



Fig. 1. Examples of oyster whole left valve (top left), left valve fragment with hinge (top right), and valve fragments lacking hinges (bottom).



Fig. 2. Locations of Garden Patch (8DI4) and Calusa Island Midden (8LL45) sites.

left valve generally attaching to the substrate.

The value of archaeological oyster assemblages to elucidating past environmental conditions and histories of human engagement with species has long been recognized within archaeology (e.g., Lawrence, 1988). Investigations of diachronic variation in archaeological eastern oyster valve size have flourished in eastern North America over the past two decades. Because oyster valve size reflects growth rate and age at death, which in turn are related to such factors as nutrient availability, environment and climate conditions, and predation pressure, oyster shells preserve a record of oyster reef health that spans many millennia (Reeder-Myers et al., 2022). Oyster height (also referred to as length), measured from the dorsal to the ventral, is strongly correlated with total shell area (Galtsoff, 1964:31–33) and is a preferred proxy for measuring valve size. Length, the longest extent perpendicular to height, is also commonly measured. Oyster height correlates to overall oyster size and is the most common metric used by biologists and archaeologists to measure oyster size and growth and to regulate the fishery (Lockwood and Mann, 2019; Rick et al., 2016; Southworth et al., 2010).

Recent meta-analyses of valve size across Indigenous shell middens, historic assemblages, and modern specimens have yielded important observations about changes through time that emphasize eastern oyster populations' resilience and the sustainability of these fisheries (Rick et al., 2016; Thompson et al., 2020). Smaller scales of study have yielded a variety of results and interpretations, including evidence of mean size decline possibly due to Indigenous harvesting pressure (Savarese et al., 2016) and climate change (Lulewicz et al., 2017), decline in the largest-sized individuals perhaps caused by historic overexploitation and environmental degradation (Hesterberg et al., 2020), and limited changes in size that could reflect long-term sustainability (Jenkins and Gallivan, 2020). Clearly, much interpretive significance rests on observable trends in oyster valve size through time.

Yet the effects of valve fragmentation on metric data collected from eastern oyster assemblages remain largely unexamined. Qualitative assessments of taphonomic grades have been used to infer live harvesting of oysters represented in middens (Savarese et al., 2016) and to assert adequate preservation of valves (Lulewicz et al., 2017:285). Rick and

colleagues (2016: SI Text, p. 2) attempted to address valve fragmentation in relation to metric data by citing Potter's (1982) analysis of whole and fragmentary valves from two assemblages on the Potomac River that yielded less than ten percent fragmentation rates. They further assert that a wide range of archaeological shell heights in their meta-analysis, from 10 mm to 189 mm, instills some confidence that whole shell measurements in the study are representative.

Assemblage fragmentation and its effects on the representativeness of surviving specimens is a longstanding archaeological concern related to human behavior and site formation processes (e.g., Collins, 1975; Nielsen, 1991; Schiffer, 1983). Zooarchaeologists have developed a range of methods for evaluating how fragmentation affects identification of taxa and elements in the archaeological record and its impact on minimum number of individuals (MNI), number of individual specimens (NISP), diversity, equitability, and various other indices and inferences (e.g., Lyman, 1994:315–338, 425–433; Lyman, 2008:250–263; Lyman et al., 1987; Randklev and Lundein, 2012). Patterns of vertebrate specimen fragmentation are not often investigated for their effects on animal size representation in assemblages. However, in several species of mollusk the problem has been addressed through allometric models estimating whole shell dimensions from hinge features (e.g., Campbell 2104; Campbell and Braje, 2015; Hillis et al., 2024; Singh and McKechnie, 2015). Ostreidae is a notable exception for which few allometric models have been developed despite the intensity of this family's archaeological study throughout the world (but see Robson et al., 2024).

Although archaeological eastern oyster shell fragmentation patterns have not been studied and published in any detail, observations made in research of other invertebrate taxa are instructive. Taphonomic studies show that mollusk shells are fragmented through a wide array of cultural and natural processes that have different effects on individual whole shell survival (e.g., Best and Kidwell, 2000a, 2000b; Hoffmeister et al., 2004; Peacock, 2000; Rick et al., 2006). The rate of shell preservation is related to shell morphology and structure, and studies of freshwater bivalves indicate that increasing sphericity and relative thickness is correlated with increasing probabilities of preservation (Wolverton et al., 2010).

These same factors are likely also germane to the preservation of all marine and estuarine bivalves, but our question here is not to understand why certain oyster valves fragment (e.g., due to differences in valve sphericity or thickness). Rather, our aim is to determine whether fragmentation has a significant effect on oyster whole valve size measurements observed in archaeological assemblages. For this purpose, we excavated and subsequently analyzed 100 % of oyster valve assemblages, focusing on the common metrics of whole valve height, length, and weight in comparison to fragmentation rates in each sampling unit and the weight of fragmented valves. Our results allow us to assess whether whole valve oyster samples alone are likely to provide representative samples for reconstructing historical ecological baselines.

3. Samples and methods

The two study assemblages are from the Calusa Island Midden and Garden Patch sites located along the Gulf coast of Florida. Both sites include extensive oyster deposits, and in each case, represent long-term oyster harvest during their Indigenous histories. The comprehensive collection and curation of left and right valves and valve fragments from the sites provide a relatively unique opportunity to assess the impact of fragmentation on assemblage whole valve size metrics.

The Calusa Island Midden site is characterized by extensive shell midden deposited from ca. 2000 BC to AD 1200 (Kangas et al., 2024). For nearly 10 years, the site has been the focus of archaeological shoreline erosion assessments by the Public Florida Archaeology Network and Florida Museum of Natural History Randell Research Center in collaboration with the Calusa Land Trust (Miller et al., 2024). The oyster assemblage used in this study is from a 50 × 50 cm column

sample excavated per stratigraphic layer spanning ca. 100 BC–AD 1200 (Kangas et al., 2024). The column sample was screened through ¼-inch hardware cloth and included 5 stratigraphic levels (Fig. 3).

The Garden Patch site is an early village and mound complex occupied ca. AD 200–1000. The oyster assemblage used in this study was excavated from Test Unit 40 near the summit center of Mound II, a shell platform dating to approximately AD 400–600 (Lulewicz et al., 2020; Singleton Hyde and Wallis, 2022; Wallis et al., 2015; Wallis and Stalter, 2021). The stratigraphic sequence consists of alternating layers of sand and shell midden of variable density and thickness. Sediments were excavated in arbitrary 10 cm levels and screened through ¼-inch hardware cloth during field collection.

Both the Calusa Island Midden and Garden Patch study assemblages were analyzed at the Florida Museum of Natural History and separated by sampling unit (e.g., level [Garden Patch] and stratum [Calusa Island Midden]). Species identification was made through comparison with modern oyster specimens available through the South Florida Archaeology and Environmental Archaeology programs comparative collections to ensure that only eastern oysters were present in the analysis. We included fragments from both oysters collected while living and those that were likely already dead and incidentally brought to the sites, with the latter accounting for less than 1 % to up to 3 % of the assemblage. All data collection was consistently performed by the same analysts per assemblage to ensure quality control and quality assessment in specimen identification and measurement protocol (e.g., Wolverton, 2013). Each oyster shell specimen was identified as a whole valve (left or right), valve fragment with a hinge (left or right), or valve fragment without a hinge (not sided). For each assemblage, all whole valves and valve fragments with hinges were counted (i.e., NISP) and weighed (g), and the MNI was calculated across non-repeating elements (e.g., hinge landmarks present). All fragments lacking a hinge were weighed but not counted. The height and length of whole valves were measured to the nearest 0.1 mm using digital calipers consistently across analysts.

3.1. Statistical analyses

All statistical analyses were performed using NCSS 22.0.6 software. The goal of analyses was to determine whether oyster valve fragmentation has a significant effect on size representation in whole valve assemblages. This goal required us to investigate the size distribution of whole valves and relationships to valve survivorship rates. Accordingly, we (1) described the whole valve size distributions, (2) evaluated how valve mean size (as represented by height) is related to valve size dispersion, which, if correlated, may reflect a bias in the sizes of valves that survived whole, and (3) calculated survival rates of whole valves. The goal also necessitated that we develop a method for estimating the mean sizes of valves before they were fragmented and compare them to whole valve size distributions. We therefore (4) estimated, based on their weight, the size of fragmented valves prior to their fragmentation, and (5) used these size estimates to account for the missing fragmented valves in the mean valve size of each sampling unit. Results approximate the effect of valve fragmentation on size representation among whole valves in each sampling unit.

3.1.1. Whole valve height comparisons

Whole left and right valve mean height and length, and respective standard deviations and coefficients of variation (CV) were calculated. Whole left valve height distributions in each sampling unit were compared by Kolmogorov-Smirnov (KS) test. To assess whether differences in overall valve size, rather than valve shape, were reflected in valve height differences, the distributions of height-length ratios (H/L) in each sampling unit were compared by KS test. To evaluate the relationship between height CV and mean height, a linear regression formula was fitted using ordinary least squares (o.l.s.).



Fig. 3. Photographs of stratigraphic profiles at Garden Patch TU 40 (left; 168 cm high) and Calusa Island Midden (right; 120 cm high).

3.1.2. Whole valve survival rates and minimum number of individuals (MNI)

Rates of whole valve survival were calculated by two methods. Survival percentage by counts (s_n) was based on the numbers of whole valves (n_z) and valve fragments with hinges (n_{fh}):

$$s_n = \frac{n_z}{n_z + n_{fh}} * 100$$

Whole valve survival percentage by weight (s_w) was calculated using the weights per sampling unit of all whole valves (w_z), all valve fragments with hinges (w_{fh}), and all valve fragments lacking hinges (w_f):

$$s_w = \frac{w_z}{w_z + w_{fh} + w_f} * 100$$

While (s_n) was calculated separately for left and right valves, (s_w) combined all valves because most valve fragments without hinges lack diagnostic features and cannot be accurately sided.

We calculated MNI using counts of the most prevalent valve ($n_z + n_{fh}$), which were lefts in all but one sampling unit. The disparity of counts between left and right valves is likely due to better preservation and more readily identifiable features on the former. We assumed that each individual organism was represented by both left and right valves in each sampling unit, and that the lower and more variable counts of right valves reflected difficulties in correctly identifying right valve fragments with hinges that were crushed beyond recognition and mistakenly categorized as valve fragments lacking hinges. We further assumed that both right and left valves of each organism were fully represented in the total oyster valve weight in each sampling unit, and that any portion of fragmented valves unrecovered during fieldwork due to spatial dispersal or decomposition was negligible. To evaluate potential imbalances in identification of fragments with hinges from left and right valves, the relationship between (s_w) and (s_n) was described by a linear regression formula fitted using o.l.s.

3.1.3. Mean valve weight

The mean whole valve weight (\bar{w}_z) for left and right valves in each sampling unit is given by:

$$\bar{w}_z = \frac{w_z}{n_z}$$

Mean weights for fragmented left and right valves are unknown because fragments lacking hinges cannot be sided. However, proportions of left and right valves among fragments lacking hinges can be estimated using valve weight trends among live collected specimens of *Crassostrea virginica*. Across various habitats in the Chesapeake region,

Marquardt et al. (2024:5) found that left valves on average comprise 56.14 % (± 0.002 SE) of dry shell weight for each organism. Their model shows a minuscule increase in left valve proportion of total weight as individuals grow larger, a trend we assume is even more negligible within the limited height range of our samples.

Based on these assumptions, we calculated a mean valve weight for fragmented left valves (\bar{w}_{lf}), which required three interim steps. First, the difference between counts of represented left and right valves (Δn) was used to equalize the fragmented sample and account for apparent discrepancies in identification. Then a corrected right valve count estimate (n_{corRfh}) was calculated from the numbers of whole left valves (n_{Lz}), left valve hinge fragments (n_{Lfh}), whole right valves (n_{Rz}), and right valve hinge fragments (n_{Rfh}):

$$\Delta n = (n_{Lz} + n_{Lfh}) - (n_{Rz} + n_{Rfh})$$

$$n_{corRfh} = (n_{Rz} + n_{Rfh}) + \Delta n$$

Second, the total weight of left valves represented in the fragmented sample (w_{estlf}) was estimated using the total weight of fragmented valves ($w_{fh} + w_f$), the total number of left fragments with hinges (n_{Lfh}), the corrected right valve count estimate (n_{corRfh}), and estimated weight proportions for left (.5612) and right (.4388) valves:

$$w_{estlf} = \frac{(w_{fh} + w_f) * (n_{Lfh} * .5612)}{(n_{Lfh} * w_{Lpro}) + (n_{corRfh} * .4388)}$$

Finally, the mean valve weight for fragmented left valves (\bar{w}_{lf}) was calculated from the estimated total weight of left valves in the fragmented sample (w_{estlf}) and the number of left valve fragments with hinges (n_{Lfh}):

$$\bar{w}_{lf} = \frac{w_{estlf}}{n_{Lfh}}$$

3.1.4. Weight and height relationships

Oyster valve weight increases exponentially with increasing height (e.g., Marquardt et al., 2024). To approximate this relationship in the 8DI4 and 8LL45 assemblages, a linear regression formula using o.l.s. was fitted to the natural logarithm (\ln) of mean weights (\bar{w}_{Lz}) and heights (\bar{H}_{Lz}) of whole left valves for each site. The log-log regression formulae were then exponentiated to convert them to the allometric formula:

$$w = aH^b$$

where (a) is the allometric coefficient, and (b) is the allometric exponent

(Campbell, 2014:306; White and Gould, 1965). The formula was converted to solve for height, and the calculated mean valve weights for fragmented left valves (\bar{w}_{Lf}) were used to predict their mean heights (\bar{H}_{Lf}):

$$\bar{H}_{Lf} = \left(\frac{\bar{w}_{Lf}}{a} \right)^{\frac{1}{b}}$$

3.1.5. Estimating effects of survivorship bias

To estimate the magnitude by which survivorship bias affects recorded valve heights, a “corrected” mean valve height (\bar{H}_{corL}) was calculated based on the proportions of whole and fragmented left valves in each sampling unit and the corresponding mean heights of whole (\bar{H}_{Lz}) and fragmented (\bar{H}_{Lf}) valves:

$$\bar{H}_{corL} = \frac{(\bar{H}_{Lf} * (100 - Sn)) + (\bar{H}_{Lz} * Sn)}{100}$$

Finally, using o.l.s., linear regression formulae were fitted to whole left valve mean height and height CV and the % difference between whole left valve mean height (\bar{H}_{Lz}) and calculated mean height of left

valve fragments (\bar{H}_{Lf}). These regressions assessed whether height and its variability in the whole valve sample were related to the magnitude of disproportionate fragmentation of valves of certain sizes.

4. Results

4.1. Whole valve height comparisons

Significant differences between sampling units in whole left valve height and length exist in both assemblages as indicated by KS tests (Fig. 4; Table 1, Table 2, Table 3). Overall, valve size appears to have increased through time at Garden Patch and decreased through time at Calusa Island Midden. At Garden Patch, valve size change is marginal except for a significant increase near the middle of the sequence, between levels M and L. Calusa Island Midden shows a series of significant declines and partial rebounds through time, with the most significant decline between strata 4 and 5.

At each site, one sampling unit is significantly different from the others in valve (H/L) (Supplement 1). At Garden Patch, the different (H/L) in Level N does not correspond with a significant height difference. At

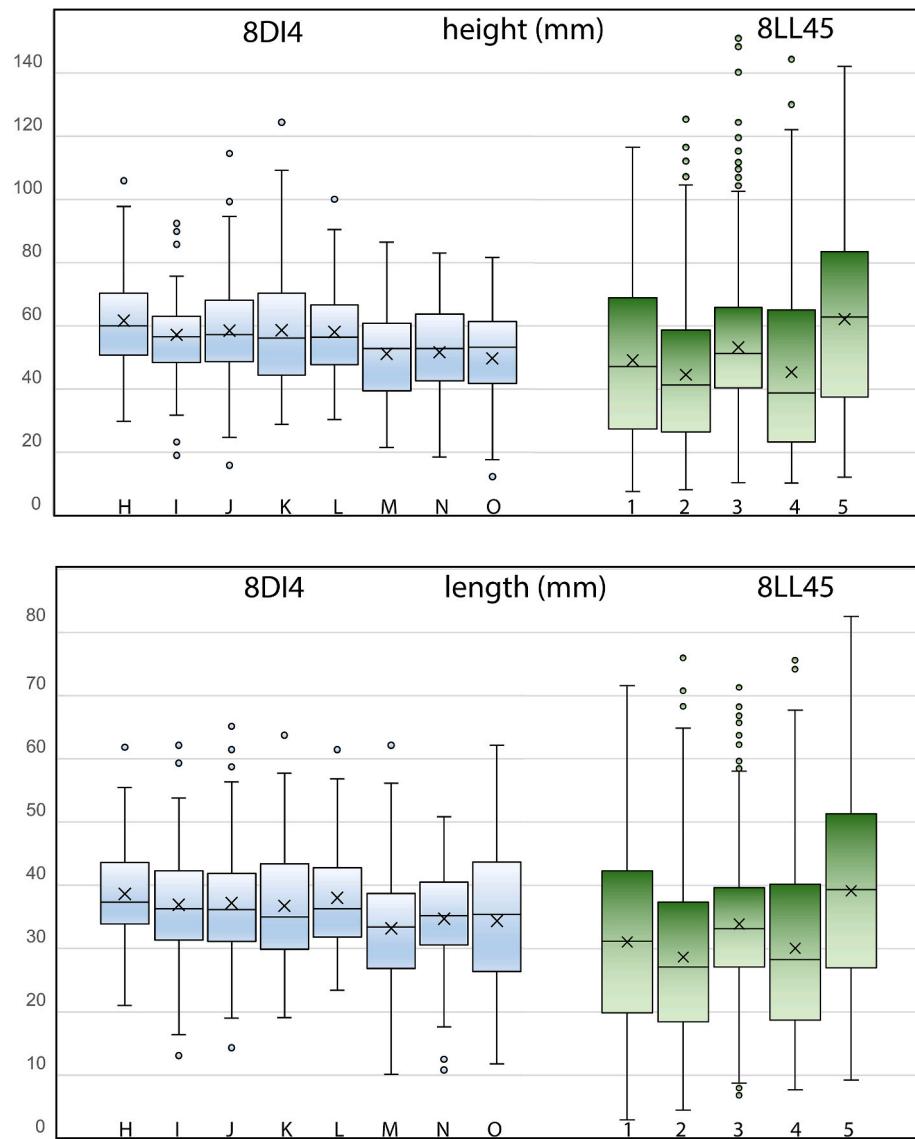


Fig. 4. Box and whisker plots comparing left valve heights and left valve lengths in each excavated context at Garden Patch (8DI4) and Calusa Island (8LL45). Plots show the median (central line), mean (x), first and third quartiles (box), and 1.5x the interquartile range whiskers. Circles represent observations beyond 1.5x the interquartile range.

Table 1

Summary of valve height and length results.

Level/Strat	Height					Length				
	Mean	SD	CV	Min	Max	Mean	SD	CV	Min	Max
Garden Patch										
H	61.72	16.61	0.27	29.9	106	38.17	8.17	0.21	21	61.8
I	57.24	15.09	0.31	19.1	92.5	36.91	9.89	0.27	13.1	62.1
J	58.56	15.97	0.27	15.9	114.6	37.18	9.31	0.25	14.3	65.1
K	58.65	18.37	0.24	28.9	124.5	36.73	10.51	0.29	19.1	63.7
L	58.14	14.04	0.26	30.4	100.1	38.00	8.24	0.22	23.4	61.4
M	51.21	16.01	0.31	21.5	86.5	33.20	9.91	0.30	10.1	62.1
N	51.70	15.88	0.31	18.5	83.1	34.71	9.09	0.26	10.8	50.8
O	49.78	17.51	0.35	12.3	81.7	34.37	12.15	0.35	11.8	62.1
Calusa Island										
1	49.16	24.98	0.51	7.7	116.6	31.08	13.75	0.44	3.0	71.6
2	44.58	22.40	0.50	8.2	125.4	28.70	13.12	0.46	4.5	76.0
3	53.31	21.70	0.49	10.5	151.1	33.90	11.06	0.33	6.9	71.3
4	45.37	24.77	0.55	10.3	144.5	30.08	13.58	0.45	7.8	75.6
5	62.15	28.13	0.45	12.1	142.1	39.16	15.29	0.39	9.3	82.5

Table 2

Probability results for Garden Patch height and length KS tests.

Height	H	I	J	K	L	M	N
I	0.333						
J	0.477	0.694					
K	0.047	0.305	0.453				
L	0.51	0.79	0.851	0.262			
M	0.005	0.14	0.005	0.037	0.029		
N	0.071	0.283	0.174	0.161	0.219	0.522	
O	0.108	0.243	0.209	0.234	0.22	0.839	0.821
Length	H	I	J	K	L	M	N
I	0.263						
J	0.099	0.997					
K	0.047	0.963	0.778				
L	0.441	0.842	0.559	0.347			
M	0.003	0.225	0.055	0.336	0.011		
N	0.359	0.544	0.625	0.568	0.545	0.512	
O	0.050	0.343	0.203	0.504	0.043	0.497	0.341

Table 3

Probability results for Calusa Island Midden height and length KS tests.

Height	1	2	3	4
2	0.000			
3	0.000	0.000		
4	0.000	0.000	0.000	
5	0.000	0.000	0.000	0.000
Length	1	2	3	4
2	0.000			
3	0.000	0.000		
4	0.019	0.022	0.000	
5	0.000	0.000	0.000	0.000

Calusa Island Midden, a small (H/L) is accompanied by a small mean height in Stratum 4, both of which are significantly smaller than those of other strata.

Variation in whole valve height and length, as measured by the CV, steadily decreases as the means of height and length increase at both sites (Fig. 5; Table 4). The coefficient of determination (R^2) shows that the CV explains most of the differences in valve height and length between sampling units at Garden Patch and most differences in valve height at Calusa Island Midden. Notably, all sampling units at Calusa Island Midden show greater dispersion in height and length compared to those at Garden Patch.

4.2. Valve survival rates and MNI

For both assemblages, the total number of left valves represented in each sampling unit is greater than the total number of right valves represented, with the exception of the smallest sampling unit (Garden Patch, Level O). As measured by counts, whole left valves vary by survival rate (s_n) from 29 % to 47 % at Garden Patch and from 23 % to 45 % at Calusa Island Midden (Table 5). For left valves, (s_n) shows strong correlations with whole valve survival rates measured by weight (s_w) (Table 6). In contrast, (s_w) is a poorer predictor of (s_n) for right valves, consistent with the assumption that right valve fragments with hinges were often misidentified as valve fragments without hinges.

Left whole valve survival rate (s_n) shows no linear relationship to valve height or height CV (Fig. 6). However, commonalities exist at the two sites in the relationship between these variables where their (s_n) coincides. For instance, small mean heights and large CVs at both sites occur in the (s_n) range of ca. 42 %–43 %. Whether such commonalities are coincidental or because (s_n) is correlated with specific taphonomic processes at both sites is currently impossible to discern due to the small number of sampling units and was not considered further.

4.3. Mean valve weight

Most sampling units at both sites have an estimated mean weight of fragmented left valves (\bar{w}_{lf}) that is less than that of measured whole left valves (\bar{w}_z) (Table 7). Three sampling units show significant disparities in which (\bar{w}_{lf}) is approximately half (levels H and J) or less than half of (\bar{w}_z) (Stratum 5). At Garden Patch, (\bar{w}_{lf}) is slightly greater than (\bar{w}_z) in Level O and at Calusa Island Midden Stratum 1 has nearly equal values for both measures.

4.4. Weight and Height relationships

The log-log relationship between whole valve mean height (\bar{H}_{lz}) and mean weight (\bar{w}_z) is well described by a regression formula for Garden Patch ($p = 0.004$) but does not reach an acceptable threshold of significance for Calusa Island Midden ($p = 0.103$; Table 8). Graphs of the exponentiated formulae illustrate additional differences between the two sites, with Garden Patch having a more gradual exponential increase in weight compared to that of Calusa Island Midden (Fig. 7). Valve weights at both sites are less than those of oysters of the same height collected live in the Chesapeake Bay region (Marquardt et al.), probably due to taphonomic effects such as leaching in archaeological specimens (Faulkner, 2011) and possibly valve growth differences reflecting specific regions and environments.

Estimated mean heights (\bar{H}_{lz}) for fragmented left valves at Garden

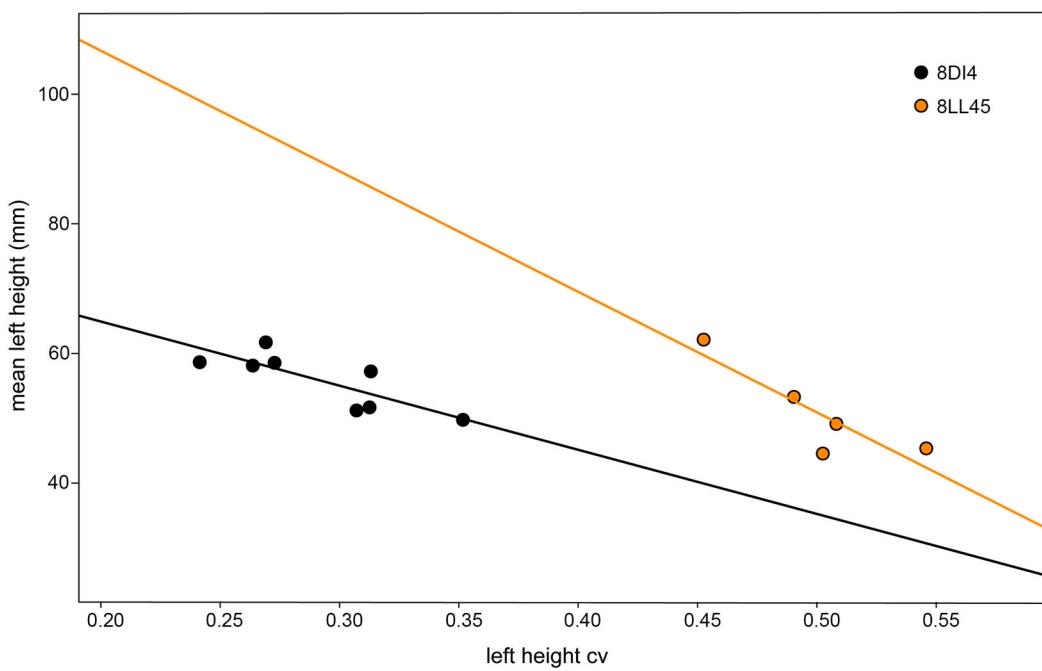


Fig. 5. O.l.s.-fitted linear regressions predicting mean left valve height from left valve height CV, and plotted values from each sampling unit.

Table 4

Linear regression models for left valve mean height and length as explained by CV.

Sample	n	R	R ²	Mean square error	t	p	equation
Garden Patch left height (Y) vs. CV (X)	8	-0.811	0.658	7.547	-3.399	0.015	$Y = 84.7041 - 98.9169X$
Garden Patch left length (Y) vs. CV (X)	8	-0.777	0.604	1.676	-3.025	0.023	$Y = 44.8865 - 32.3148X$
Calusa Island left height (Y) vs. CV (X)	5	-0.871	0.759	16.537	-3.075	0.054	$Y = 143.8917 - 185.9996X$
Calusa Island left length (Y) vs. CV (X)	5	-0.620	0.384	13.785	-1.368	0.265	$Y = 51.5494 - 45.6902X$

Table 5

Counts and weights of whole and fragmented valves, and percent survival of whole right and left valves (Sn).

Level/ Strat	Depth (cm)	MNI	Left whole		Right whole		Left fragment w/hinge		Right fragment w/hinge		fragments lacking hinge (n)	Left Valve Survival (%)	Right Valve Survival (%)
			n	g	n	g	n	g	n	g			
Garden Patch													
H	70–80	154	57	910.1	36	335.9	97	405.7	53	168.7	1067	37.01	40.45
I	80–90	231	59	840.8	75	683	172	782.6	100	419.1	1398	25.54	42.86
J	90–100	340	158	2562.1	115	1300.1	182	553.6	126	386.1	2039.7	46.47	47.72
K	100–110	222	86	1502.9	75	820	136	481.6	95	353.5	1922.5	38.74	44.12
L	110–120	244	91	1620.2	97	873.9	153	703.2	94	397.5	1864.1	37.30	50.79
M	120–130	231	94	1258.9	113	856.9	137	607.4	59	233.4	1219.7	40.69	65.70
N	130–140	86	37	538.2	44	318.1	49	186.2	27	99.5	651.4	43.02	61.97
O	140–150	87	28	360.8	48	337.6	39	210.6	39	113.7	434.4	41.79	55.17
Calusa Island													
1	0–53	1890	453	5080.24	526	5715.27	1437	8981.14	913	4989.52	13970.66	23.97	36.55
2	53–62	2452	559	5170.96	757	5352.4	1893	8799.7	937	4445.21	10976.95	22.80	44.69
3	62–87	2057	676	6259.58	603	4717.37	1381	5987.43	876	3991.62	8255.39	32.86	40.77
4	87–112	2961	1276	14424.25	1691	10341.92	1685	6441.02	647	4354.49	5352.4	43.09	72.33
5	112–120	448	201	5170.96	175	2449.4	247	2902.99	130	1360.78	1360.78	44.87	57.38

Patch range from 38.3 mm to 52.4 mm (Fig. 8). At Calusa Island Midden, (\bar{H}_{Lz}) ranges from 42.6 mm to 50.5 mm (Fig. 9). The % difference of estimated mean height for fragmented valves compared to measured whole valves ranges from +5 % to −47 % at Garden Patch and from 0 % to −22 % at Calusa Island Midden (Table 7).

4.5. Estimating effects of survivorship bias

The percent difference between mean whole valve height (\bar{H}_{Lz}) and

estimated mean heights of fragmented valves (\bar{H}_{Lf}) explains two-thirds of the variation in mean whole valve height at Garden Patch (Fig. 10; Table 9). Whole valve mean height (\bar{H}_{Lz}) increases as the estimated fragmented valve mean height (\bar{H}_{Lf}) becomes smaller in comparison. An analogous relationship between these variables may also apply to Calusa Island Midden but is not significant ($p = 0.17$). At Garden Patch, whole valve height CV declines as fragmented valve mean heights (\bar{H}_{Lf}) become smaller relative to that of whole valves (\bar{H}_{Lz}), albeit with a weaker correlation ($R^2 = 0.40$; $p = 0.091$).

Table 6

Linear regression models for left and right valve survival rates (S_n) at each site as explained by proportions of whole valve survival as measured by weight (S_w).

Sample	R	R^2	Mean square error	t	p	equation
Garden Patch left valves	0.927	0.859	6.365	6.041	0.001	$S_n = -8.9428 + 1.02083S_w$
Garden Patch right valves	0.459	0.211	77.524	1.267	0.252	$S_n = 16.1409 + .74709S_w$
Calusa Island Midden left valves	0.975	0.951	7.035	7.596	0.005	$S_n = 5.393 + .6577S_w$
Calusa Island Midden right valves	0.918	0.842	45.055	4.004	0.028	$S_n = 12.7206 + .8774S_w$

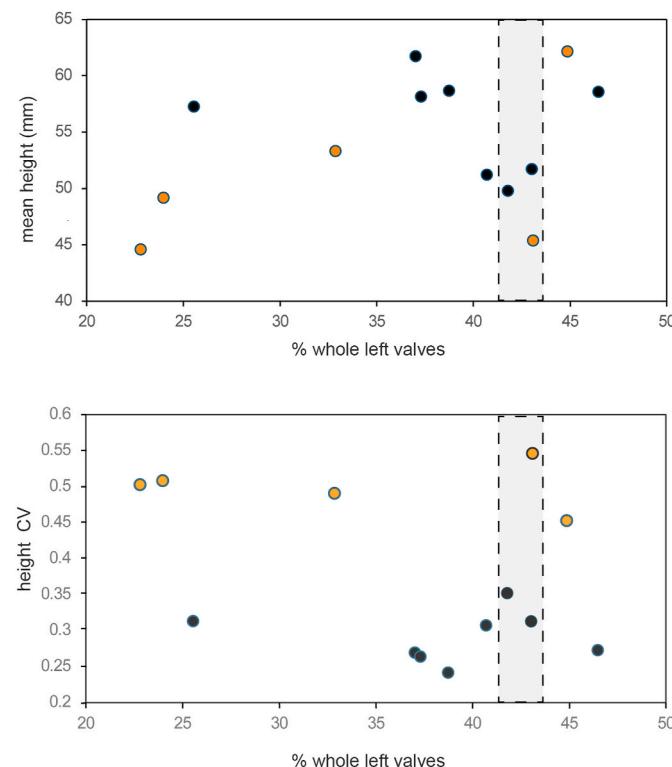


Fig. 6. Bivariate plot of % whole left valves (S_n) and mean height and CV for each sampling unit (Garden Patch = black; Calusa Island Midden = orange). (S_n) of 41.5 %–43.5 % is highlighted. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

A comparison of whole valve mean heights (\bar{H}_{Lz}) and “corrected” mean heights (\bar{H}_{corL}) for each sampling unit shows that accounting for fragmentation significantly alters perceived diachronic changes in valve size (Fig. 11). At both sites, the magnitude of difference between sampling units is reduced in the “corrected” heights. At Garden Patch, the overall trend of increasing size through time is reversed in the corrected data, with the largest (\bar{H}_{Lz}) in Level H becoming the smallest (\bar{H}_{corL}), and the formerly smallest (\bar{H}_{Lz}) of Level O becoming the largest (\bar{H}_{corL}). At Calusa Island Midden, diachronic trends in (\bar{H}_{Lz}) are mirrored in (\bar{H}_{corL}) but differences between sampling units are diminished in all cases except between Stratum 2 and Stratum 1.

5. Discussion

This study demonstrates that whole oyster valve archaeological assemblages can suffer from substantial survivorship bias in which the mean size of valves that fragment is significantly different than that of valves that survive whole. This result should encourage skepticism of oyster valve size research that does not consider the effects of valve fragmentation. It also highlights the need to develop methods for estimating oyster whole valve size from valve fragments.

Our whole valve sampling units show differences in height and length that are statistically significant and on a similar scale to many high-profile studies (e.g., Hesterberg et al., 2020; Rick et al., 2016; Thompson et al., 2020). But our calculations show that survivorship bias likely exaggerates some height differences at Calusa Island Midden and reverses true trends in height at Garden Patch.

There are many assumptions built into our method of accounting for fragmentation that limit its suitability for making precise and accurate corrections. We assumed left and right valves were represented in equal proportions, but in some cases, they might be unequal due to cultural (e.g., Jenkins, 2017) or natural processes. Though we used a constant mean weight ratio between left and right valves, this ratio varies among individuals and could differ by habitat or region. Our regression formulae predicting valve height from valve weight are based on means rather than individual measurements, which greatly limit sample sizes for the models and increase their error. Perhaps most limiting is the fact that our method cannot deduce valve size variation within sampling units of fragmented valves, which prevents statistical assessments of difference in “corrected” valve heights between sampling units.

Despite these imperfections as a bias correction tool, the consistency of results across several dimensions of the data demonstrates that the method does well at identifying survivorship bias and approximating its confounding effects. Correlation between the increasing mean valve height and its diminishing variation (CV) at both sites is consistent with survivorship bias. We hypothesize that this relationship shows the effect of fragmented small valves not being included in whole valve height measurements. As rates of fragmentation become increasingly lopsided by size class, with mostly small valves being fragmented, the height variation of whole valves narrows and the mean height increases.

This hypothesis is validated by the correlation of whole valve height and its difference from estimated fragmented valve height. The estimated fragmented valve height approximates the measurements that are missing from the whole valve sample in each sampling unit. Whole valve mean height increases predictably with growing disparities between whole and fragmented valve mean height estimates, indicating that inequitable fragmentation of valves by size class has a significant impact on the size distribution of the whole valve sample. This correlation also corroborates our method and assumptions for estimating heights (\bar{H}_{Lz}) of fragmented left valves, at least for Garden Patch.

The weakness of this relationship at Calusa Island Midden is likely due in part to the smaller number of sampling units that lead to higher regression model error. In addition, compared to Garden Patch, Calusa Island Midden shows less pronounced patterns of fragmentation linked to valve size, as reflected in the overall larger whole valve height CVs and their weaker correlation with mean valve height. The shapes of whole valves in one sampling unit, Stratum 4, are different from the others, which may be associated with different fragmentation patterns than other strata. We therefore expect Calusa Island Midden sampling units to suffer less from size-related patterns of survivorship bias than those at Garden Patch, and the smaller differences between (\bar{H}_{Lz}) and (\bar{H}_{corL}) bear out these expectations.

5.1. Implications of study

This case study evaluates how fragmentation patterns influence the sizes of measured archaeological oyster valves with implications for

Table 7

Results of calculations estimating mean heights of broken left valves (\bar{H}_{Lf}) and comparison to mean heights of whole left valves (\bar{H}_{Lz}).

Left $n_z + n_{fh}$	Right $n_z + n_{fh}$	Δn	n_{corRfh}	n_{LiH}	w_{estLf}	\bar{w}_{Lf}	\bar{w}_{Lz}	\bar{H}_{Lf}	\bar{H}_{Lz}	% difference \bar{H}_{Lf} and \bar{H}_{Lz}	
Garden Patch											
H	148	89	59	112	97	862.95	8.90	17.85	38.42	61.72	-46.53
I	231	175	56	156	172	1521.55	8.85	14.25	38.27	57.24	-39.72
J	340	241	99	225	182	1515.58	8.33	16.22	36.75	58.56	-45.77
K	222	170	52	147	136	1495.08	10.99	17.48	44.30	58.65	-27.88
L	244	191	53	147	153	1693.57	11.07	17.80	44.51	58.14	-26.57
M	231	172	59	118	137	1231.69	8.99	13.39	38.69	51.21	-27.84
N	86	71	15	42	49	561.25	11.45	14.55	45.54	51.70	-12.66
O	67	87	-20	19	39	549.54	14.09	12.89	52.35	49.78	5.04
Calusa Island Midden											
1	1890	1439	451	1364	1437	16043.73	11.16	11.21	49.08	49.16	-0.16
2	2452	1694	758	1695	1893	14251.97	7.53	9.25	43.42	44.58	-2.63
3	2057	1479	578	1454	1381	10004.86	7.24	9.26	42.90	53.31	-21.64
4	2961	2338	623	1270	1685	10163.31	6.03	11.30	40.52	45.37	-11.29
5	448	305	143	273	247	3018.27	12.22	25.73	50.48	62.15	-20.72

Table 8

Linear regression models for left valve whole ln mean weight and whole ln mean height.

Sample	n	R	R ²	Mean square error	t	p	equation
Garden Patch	8	0.883	0.780	0.005	4.614	0.004	$Y = -3.2048 + 1.4778X$
Calusa Island Midden	5	0.801	0.642	0.086	2.319	0.103	$Y = -7.3228 + 2.5062X$

subsequent interpretations of oyster population health or harvest sustainability. In light of these results, can archaeological oyster size studies make valid observations of trends in time and space without considering the effects of fragmentation?

At Garden Patch, our results indicate that whole oysters do not provide a representative sample and that considering them in isolation would lead to erroneous conclusions. An archaeologist considering only whole valves would observe a significant size increase over time that might be interpreted as an example of Indigenous long-term sustainable

harvest. In this case, however, the differences between whole valve mean sizes are determined primarily by assemblage fragmentation patterns. The corrected mean heights for Garden Patch offer a contradictory result, suggesting an overall valve size decline over time rather than an increase.

The Calusa Island Midden sampling units appear to suffer less from survivorship bias than those from Garden Patch. Nonetheless, corrected mean heights demonstrate a moderated series of changes that may be less significant compared to those observed in the whole valve mean heights. The corrected mean heights of two strata, 1 and 2, are similar to their respective whole valve mean heights. This correspondence would occur if the whole valve measurements were representative of these sampling units. Alternatively, the whole valve and fragmented valve sample populations could be quite different, such as if very large and very small valves were disproportionately fragmented and together have the same mean as whole mid-size valves. The relatively high CV of the whole valve samples and their consistency with the CVs of other sampling units at the site make such a scenario unlikely.

These results show that fragmentation can be an important driver of size representation across whole valves, and we cannot assume that the sizes of whole oyster valves in each archaeological assemblage are representative of the original oyster population at the time of harvest in

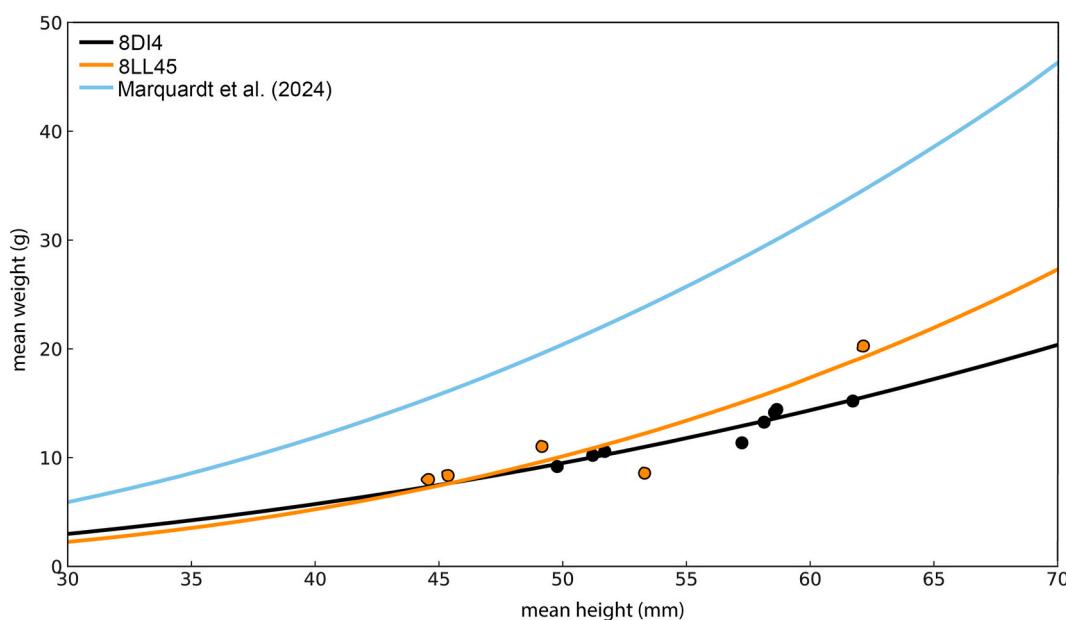


Fig. 7. Exponential regression curves predicting the relationship between left valve weight and height for live collected specimens in the Chesapeake Bay region and archaeological specimen means at Garden Patch (8DI4) and Calusa Island Midden (8LL45).

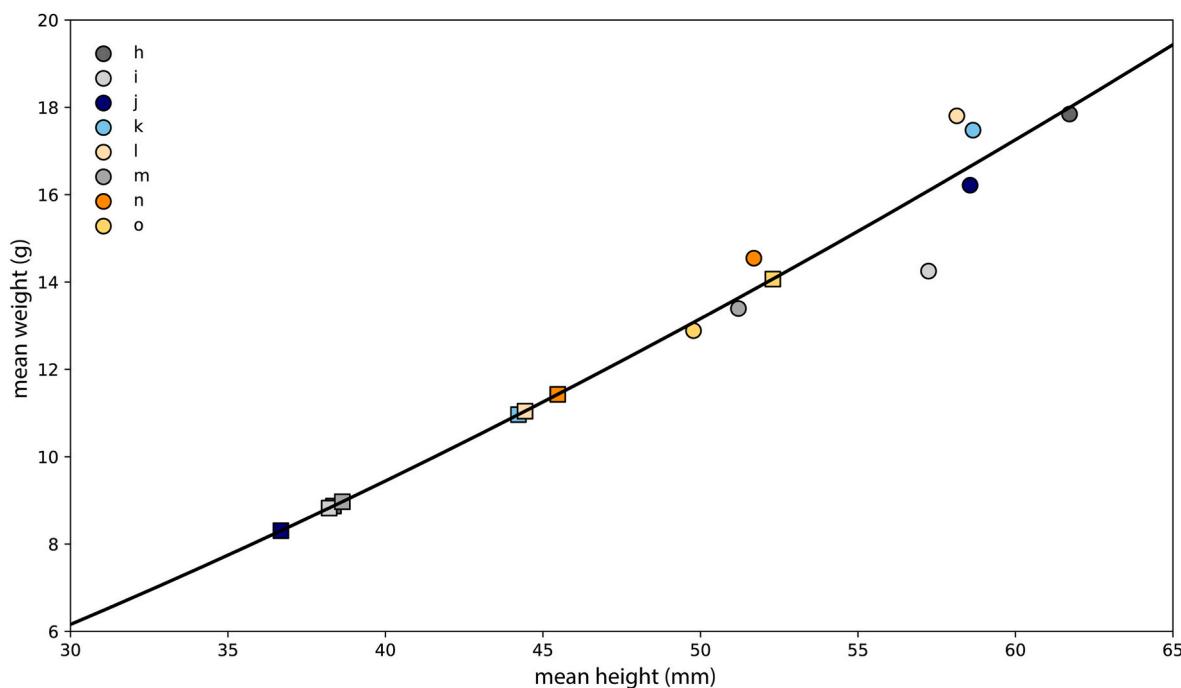


Fig. 8. Exponential regression curve predicting relationship between left valve mean weight and mean height at Garden Patch and plots of whole valve means (circles) and predicted fragmented valve means (squares). $Y = (0.03928886)X^{(1.48618)}$.

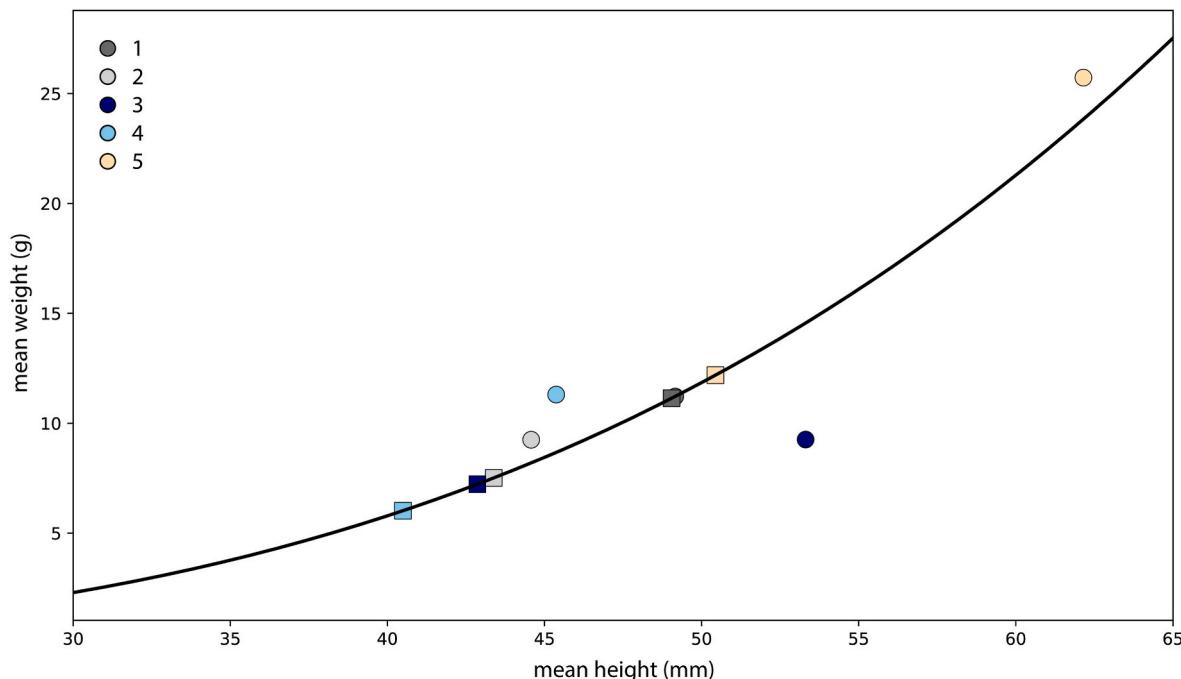


Fig. 9. Exponential regression curve predicting relationship between left valve mean weight and mean height at Calusa Island Midden and plots of whole valve means (circles) and predicted fragmented valve means (squares). $Y = (4.128044 \times 10^{-5})X^{(3.212481)}$.

the past. This conclusion contributes to a broader zooarchaeological concern with understanding sources of variation in the attributes we are measuring (e.g., Reitz et al., 2009). Failing to consider survivorship bias for each sampling unit, as is currently commonplace among researchers of archaeological eastern oyster — including some members of the author team — leaves us blind as to which metrics and which comparisons are likely to be erroneous, hindering conclusions about historical ecological baselines.

Our results also demonstrate that fragmentation rates and their

effects are variable not only between sites but also within sampling units from the same site, contributing differently to whole valve representation depending on context. While this study suggests fragmentation is a significant source of variation in oyster size at single sites, it remains to be seen how these processes may affect meta-analyses drawing on groups of sites across a large region (e.g., Rick et al., 2016; Thompson et al., 2020).

It is also important to note that while reconstructing oyster and other shellfish size is a valuable metric for archaeologists, biologists, and

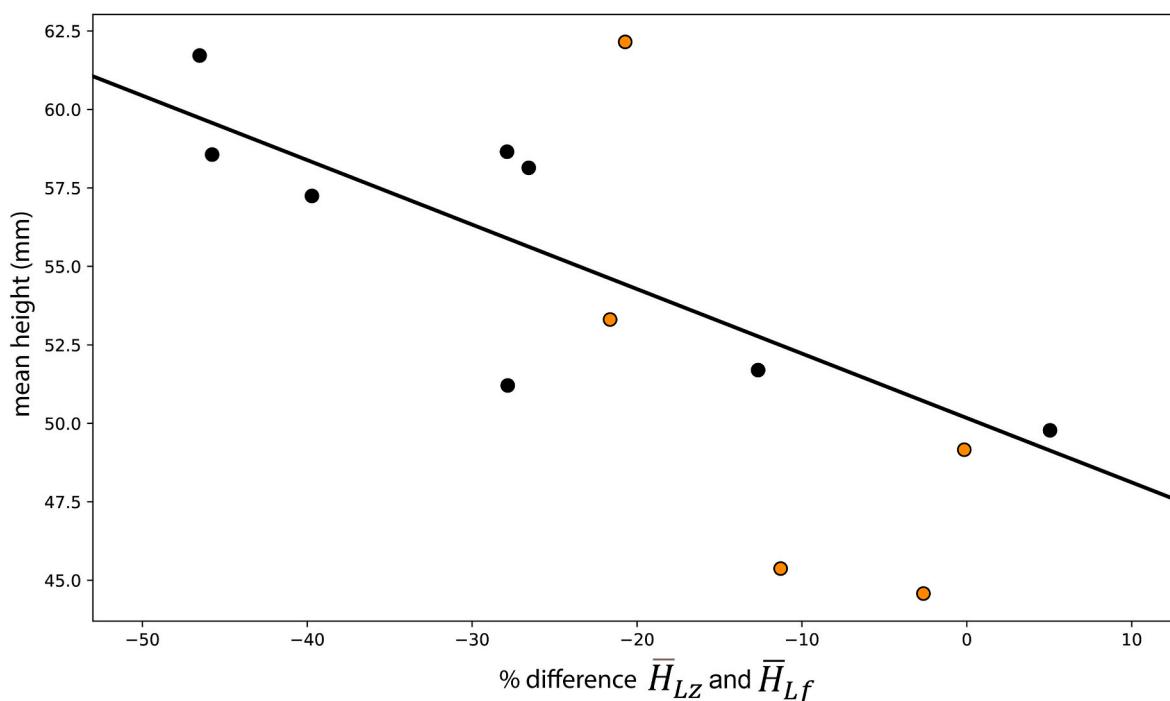


Fig. 10. O.l.s.-fitted linear regression predicting whole mean left valve height from the difference between whole left valve mean height (\bar{H}_{Lz}) and predicted mean height of fragmented left valves (\bar{H}_{Lf}) at Garden Patch. Values from sampling units at Garden Patch (black) and Calusa Island Midden (orange) are also plotted. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 9

O.l.s. linear regression for mean height (\bar{H}_{Lz}) and CV vs. % difference of \bar{H}_{Lz} and \bar{H}_{Lf} .

Sample	R	R ²	Mean square error	t	p	equation
Garden Patch left height	-0.819	0.671	7.258	-3.501	0.013	y = 50.2002 - 0.2046X
Garden Patch height CV	0.635	0.403	0.001	2.014	0.091	y = 0.3275 + .0013005X
Calusa Island left height	-0.719	0.517	33.138	-1.793	0.171	y = 45.0506 - .51945X
Calusa Island Midden height CV	0.494	0.244	0.001	0.983	0.398	y = 0.5187 + .00167X

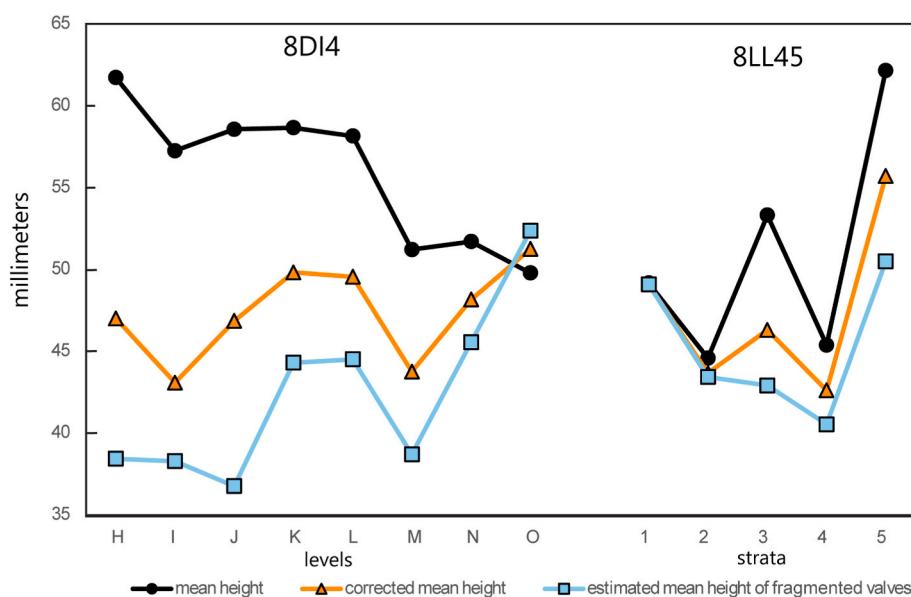


Fig. 11. Whole left valve mean height (\bar{H}_{Lz}), predicted mean height of fragmented left valves (\bar{H}_{Lf}), and corrected mean left height (\bar{H}_{corr}) for each sampling unit.

others seeking to understand the long-term effects of human predation and environmental change on shellfish populations, oyster age is also relevant to consider in such efforts. Recent archaeological studies of oyster age from *O. edulis* in Denmark, for example, highlight the need for continuing to seek other metrics for evaluating the historical ecology of eastern oysters (Robson et al., 2024). Estimating ages for ancient *C. virginica* is promising when using isotope sclerochronology but remains a challenge when applied across large geographic areas and is an area in need of further research (Zimmt et al., 2019). Such age estimates can be placed in tandem with size reconstructions to look at long-term patterns in shellfish growth rates, further emphasizing the need for robust taphonomic studies of oyster and other shellfish.

Ultimately, our study is a call for expanding studies of oyster and other shellfish taphonomy, inclusive of controlling for confounding factors. Recent comparisons of archaeological oysters to contemporary wild and farmed oysters in Florida is an important step in this direction (Rogers et al., 2025). Site formation processes and taphonomy have long played an important role in shell midden research (Rick, 2024) and studies like ours demonstrate that these foci must remain central to the continued development of shell midden archaeology and its interpretive power. Accounting for fragmentation in oyster valve size studies has the potential to yield more precise and accurate measurements of past population valve sizes and more realistic assessments of their temporal and spatial variation, thereby refining baselines and offering conservation managers and other stakeholders better clarity for evaluating historical ecological data. Doing so will require collecting data differently, including different approaches to field excavation and curation of oyster assemblages and, where possible, revisiting existing primary data. In the interest of developing protocols for analysis that include fragmentation considerations, we suggest that future studies incorporate the following components.

1. The CV of whole valve height and length are useful for assessing the potential for survivorship bias. Relatively small CVs may correlate with significantly disproportionate fragmentation of valves of specific sizes. Conversely, large CVs may indicate that fragmentation is more equally distributed among valves of different sizes. Yet even among sampling populations with significant dispersion, if CVs are correlated with height and length of whole valves, as in the present study, effects from survivorship bias are indicated and analysis of fragmented valves is required.
2. Excavating, collecting, and counting whole valves and valve fragments is essential for determining survival rates of whole valves and estimating the weight and size of fragmented valves. These counts are also consistent with MNI calculations based on non-repetitive elements (NRE) (but see Giovas, 2009).
3. Weighing oyster shell of distinct fragment classes—whole valves, valve fragments with hinges, and valve fragments without hinges—is informative as a proxy for the size of fragmented valves. We have shown that the relationship between valve weight and height of whole valves can be used to approximate the size distribution of the fragmented valve population before it was fragmented. Developing more robust regression models from a bevy of individually weighed whole valves at each locality would help improve the accuracy of these corrections. In addition, the effects of screen size or other systematic sampling procedures on fragmented valve weight estimates are currently unclear and need to be investigated.
4. Finally, to transcend the challenges presented here and to determine more accurately if reconstructing oyster size from fragmented shells has a strong difference from those relying only on whole valves, developing regression formulae for estimating whole valve size from the hinge area should be prioritized. Such studies have proven important for mussels, clams, and other species (Campbell and Braje, 2015; Hillis et al., 2024; Singh and McKechnie, 2015). A preliminary attempt at doing this for eastern oysters did not yield statistically

significant results (Rick et al., 2016), but a more robust sample is needed to further test the feasibility of building such a model.

6. Conclusion

This study demonstrates that archaeologists need to carefully consider the role of assemblage fragmentation to ensure the accuracy of data regarding oyster valve size variation in the past. Improving the representativeness of measured valve samples will significantly enhance the value of results for informing historical ecological baselines. We encourage continued critical evaluation of the archaeology and paleobiology of oyster assemblages and interrogation of their historical ecological implications in the present. In many instances, this will include adjustments to the excavation, collection, curation, and laboratory analysis of oyster assemblages that is inclusive of whole valves, valve fragments with hinges, and valve fragments without hinges. While focused on eastern oysters, our findings likely apply to other mollusks, and we encourage researchers working on the historical ecology of shellfish around the world to conduct taphonomic analyses to continue to refine their datasets and create more robust interpretations of the human-environment interactions represented.

CRediT authorship contribution statement

Neill J. Wallis: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Torben C. Rick:** Writing – review & editing, Writing – original draft, Conceptualization. **Cristina I.R. Oliveira:** Writing – review & editing, Methodology, Investigation. **Alisa Luthra:** Writing – review & editing, Investigation. **Jennifer Green:** Writing – review & editing, Project administration, Methodology, Investigation, Data curation. **Aditi Jayarajan:** Investigation. **Michelle J. LeFebvre:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2025.106335>.

Data availability

The data that support the findings of this study are included as part of the paper and supplementary materials.

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