BioOne COMPLETE

Dying, Decaying, and Dissolving into Irrelevance: First Direct in-the-Field Estimate of Crassostrea virginica Shell Loss—a Case History from Mississippi Sound

Authors: Pace, Sara M., Poussard, Leanne M., Powell, Eric N., Ashton-Alcox, Kathryn A., Kuykendall, Kelsey M., et al.

DYING, DECAYING, AND DISSOLVING INTO IRRELEVANCE: FIRST DIRECT IN-THE-FIELD ESTIMATE OF *CRASSOSTREA VIRGINICA* SHELL LOSS—A CASE HISTORY FROM MISSISSIPPI SOUND

SARA M. PACE,[1]* LEANNE M. POUSSARD,[1] ERIC N. POWELL,[1] KATHRYN A. ASHTON-ALCOX,[2] KELSEY M. KUYKENDALL,[1] LAURA K. SOLINGER,[1] KATHLEEN M. HEMEON[1] AND THOMAS M. SONIAT[3]

[1]*Gulf Coast Research Laboratory, University of Southern Mississippi, 703 East Beach Drive, Ocean Springs, MS 39564;* [2]*Haskin Shellfish Research Laboratory, Rutgers University, 6959 Miller Ave., Port Norris, NJ 08349;* [3]*Department of Biological Sciences, University of New Orleans, 2000 Lakeshore Drive, New Orleans, LA 70148*

ABSTRACT A mass mortality event that occurred in the Mississippi Sound in September 2016 provided an opportunity for the first natural field study of the rate of taphonomic loss of oyster shell. At the Pass Christian Reef, limited recruitment in the years following the mortality event resulted in little shell addition over a 2.67-y period, thereby permitting a direct comparison between shell present as living oysters in August 2016 and dead shell collected in April/May 2019. By April 2019, most oyster shell valves were riddled with holes, some of which perforated the valves. Deterioration of the shell surface was ubiquitous, and edge erosion was commonplace. Left valves were preferentially preserved: the left valves comprised 67% of the intact valves and 85% of the minor fragments after 2.67 y. Thus, at the time of collection, minimally 50% of the right valves originally present on the reef had disappeared. The increased differential between left and right valves of the minor fragments suggests a continuing differential in preservation, leading to cultch being overwhelmingly represented by left valves. Based on estimates derived from changes in shell weight at length and estimates of right-valve loss, by April 2019, between 30% and 51% of the carbonate originally added to the reef in 2016 was lost, yielding an estimated oyster shell half-life of between 2.6 and 5.1 y in the Mississippi Sound. The half-lives estimated from this first infield experiment fall precisely within the range of previous less direct estimates from laboratory experiments or survey time series. Oyster shell degrades rapidly: case histories now include a wide latitudinal range and a wide temperature range, which suggests that these rapid shell degradation rates are the norm over most of the range of the eastern oyster. Understanding the impermanence of oyster shell is crucial to the sustainable management of oyster reefs, as the addition of shell to the reef framework must balance rapid shell degradation rates to prevent stock collapse and ultimately the loss of reef structure.

KEY WORDS: taphonomy, shell loss, *Crassostrea virginica*, Mississippi Sound

INTRODUCTION

Carbonate input by bivalve shell formation into marine and estuarine sediments is quantitatively comparable to the production of wood by trees in a forest (Gutiérrez et al. 2003). Sedimentary carbonate is ecologically important in providing habitat (Kidwell 1986, Coen et al. 2007), refuge from predation (Guay & Himmelman 2004, Coen et al. 2007), and buffering capacity against acid production from sulfide oxidation (Green et al. 1998, 2004). Bivalve shells persist on siliciclastic continental shelves and estuaries over ecological time, as evidenced by the fact that the major contributor to death assemblages is bivalve shell (Staff et al. 1985, Best 2008, Kidwell 2008), with a lesser but important contribution by echinoderms in some areas (Lebrato et al. 2010). Shell production and degradation are ubiquitous processes in marine sediments across a variety of environments of deposition (Powell et al. 2011).

Calculation of shell production can reliably measure the input of carbonate into the sedimentary environment (Beukema 1980, Powell 1992, Powell et al. 2012b). Most marine molluscan assemblages produce 50–1,000 g $CaCO_3$ m^{-2} yr^{-1}, and production by oysters alone is estimated at 90,000 g $CaCO_3$ m^{-2} yr^{-1} (Smith 1971, Powell et al. 1989, Gutiérrez et al. 2003). Oysters, being significant contributors to carbonate production in estuarine environments (Powell et al. 2012, Waldbusser et al. 2013), play an important role in global carbonate budgets and are capable of producing carbonate in highly variable and thermodynamically unfavorable environments (Waldbusser et al. 2011).

Oyster reefs provide important ecosystem services by introducing complexity into an environment and, thereby, increasing species abundance and richness (Stunz et al. 2010, Kingsley-Smith et al. 2012). Oyster reefs also affect water flow and water quality, and provide a food resource for a range of commercially important species (Peterson et al. 2003, Grabowski et al. 2012, Kaplan et al. 2016, Darrow et al. 2017). Unfortunately, oyster shell does not appear to be a permanent resource. Rather, shell breaks down over time, requiring the deaths of oysters to continually supply shell to the reef. The death of oysters creates a positive feedback loop by increasing the amount of shell available on reefs, which then fosters increased settlement of larvae and increased habitat complexity sheltering larvae from predation, increasing the likelihood that the larvae survive into adulthood (Mann et al. 2009a, Southworth et al. 2010, Powell et al. 2012), thereby ultimately increasing the rate of shell addition.

Today, shell loss from degradation likely exceeds shell gain in oyster reefs worldwide, as seen in larger east coast estuaries such as the Chesapeake Bay (Harding et al. 2011, Mann et al. 2009a, Southworth et al. 2010) and Delaware Bay (Powell et al. 2012). This explains in some measure the worldwide loss of

oyster reef acreage, including loss in most U.S. estuaries (Beck et al. 2009, zu Ermgassen et al. 2012). When more shell is lost than is added to the reef, a negative feedback loop is created as recruitment is thereby reduced, ultimately resulting in the reduction of adults with the subsequent reduction in adult deaths, and thus a lower rate of shell addition to the reef (Powell et al. 2007, 2012).

Biological interactions, bioenergetics of shell formation, and characteristics of the surrounding environment determine how shell material dissolves or is preserved (Carriker et al. 1980, Best & Kidwell 2000, Callender & Powell 2000, Powell et al. 2008). Shells degrade and reenter the carbonate cycle as a result of taphonomic processes such as bioerosion, abrasion, fragmentation, and dissolution acting on the shell surfaces (Gunter et al. 1957, Warburton 1958, Powell et al. 2006, Waldbusser et al. 2011, Carroll et al. 2015). Shell preservation is encouraged by rapid burial, protective periostrical coats, carbonate saturation, and carbonate polymorph for which low-Mg calcite normally is best preserved (Bottjer & Carter 1980, Cai et al. 2006, Parsons-Hubbard et al. 1999, Powell et al. 2012b, Foote et al. 2015).

For oyster shell, shell loss results primarily from bioerosion, fragmentation, and dissolution. Primary bioeroders include clionid sponges and spionid worms (Carver et al. 2010, Diez et al. 2013, Carroll et al. 2015). Shell fragmentation commonly occurs (Lawrence 1968, Elner & Lavoie 1983, Zuschin et al. 2003) and is often the result of bioerosion or predation. Smaller shell fragments, having higher surface to volume ratios, are presumed to have increased rates of dissolution (Cummins et al. 1986, Kidwell 2001). By contrast, shell polymorph should increase preservability. Oddly enough, with the exception of the adductor muscle attachment site (Lee et al. 2011) and the cement-binding oysters together in clumps (MacDonald et al. 2010), oyster shell is composed of low-Mg calcite (Esteban-Delgado et al. 2008, Ivanina et al. 2013), yet oyster shell degrades rapidly compared with other molluscan shell on the seafloor (Parsons-Hubbard et al. 1999, Callender & Powell 2000, Powell et al. 2008, Kosnik et al. 2009). In the Delaware Bay and Chesapeake Bay, the half-life of oyster shell has been estimated to be between 3 and 10 y (Powell et al. 2006, Mann et al. 2009a, Powell et al. 2012a, Waldbusser et al. 2013). The rates are consistent with rates of dissolution observed in laboratory experiments (Waldbusser et al. 2011, Ries et al. 2016). In fact, estimates of the rate of oyster shell breakdown exceed that of any other bivalve except mussels (compare Callender et al. 1994, Powell et al. 2006, 2011, Best et al. 2007).

Processes abetting rapid shell loss include a low rate of burial; higher rates of burial are associated with shell preservation (Powell 1992, Davies et al. 1989, Powell et al. 2012a, 2012b). The rapid degradation of oyster shell is consistent with the tendency for shell exposed on carbonate-rich sediments and hard grounds to degrade more rapidly than shell in siliciclastic sediments (Best & Kidwell 2000, Best 2008, Powell et al. 2008). Speculation also focuses on the observation of chalky deposits naturally occurring in oyster shell (Margolis & Carver 1974, Chinzei 2013, Vermeij 2013), which may in part yield the lower shell density and less resistance to fracture in comparison with other bivalves (Taylor & Layman 1972, Price et al. 1976). Regardless, in the mid-Atlantic, reef accretion requires that the oyster population be near carrying capacity if shell loss rates are accurate (Powell et al. 2012a).

The dramatic loss of oyster reef since the 1800s has resulted in the development of a range of models for sustainable management of the fishery (Powell et al. 2018). Most do not consider the shell bed explicitly (e.g., Klinck et al. 2001, Weber et al. 2013, Wilberg et al. 2013, Kjelland et al. 2015), but many recent models include management of the shell bed (Powell et al. 2007, 2012a, Soniat et al. 2012, 2014, Moore et al. 2018). These models require specification of the rate of shell loss. Although a number of estimates now exist and are in general agreement, these rates come from laboratory experiments and estimates from field survey time series. Although rates of shell loss have been measured directly in the field for a number of species (e.g., Callender et al. 1994, Kennish & Lutz 1999, Best et al. 2007, Krause et al. 2011, Powell et al. 2011, Edinger & Sherwood 2012, Klompmaker et al. 2017), no such measurement exists for oyster shell, and, consequently, the rate of shell loss remains a substantive uncertainty in developing sustainable management options for oyster reefs.

Oysters are susceptible to mass mortality events which, under select circumstances, might provide a direct in-field measurement of the rate of shell degradation. A mass mortality event affecting the eastern oyster *Crassostrea virginica* occurred in the Mississippi Sound in 2016. One of the reefs affected was the Pass Christian Reef (MDMR 2013). Maghan (1967), Ogle (1979), and Eleuterius (1977) provide regional overviews. Before September 2016, surficial shell on the Pass Christian Reef was almost entirely contributed by live animals; very little cultch was present. Sampling during the previous months (February–August) showed that oyster clumps were abundant and oyster densities were high. By September 2016, no live animals were present on this reef or in the surrounding area. The proximate cause of the demise was a low-oxygen event influencing a population with a low condition index typical for late summer in the Mississippi Sound. Recruitment was limited over the subsequent years (October 2016 to April 2019) despite population recoveries at nearby reefs. Thus, very few animals lived, died, and added shell to the shell bed between October 2016 and April 2019. The attributes of the oyster population both at the time of mortality and subsequently provided an opportunity for the first direct field measurement of oyster shell taphonomic rates, the results of which are presented here.

MATERIALS AND METHODS

Sample Collection

Four oyster reefs in the western Mississippi Sound, including the Pass Christian Reef, were sampled between February and August 2016, once in February and March, bimonthly in April, and monthly from May forward. Sampling stopped following November 2016 and resumed in July 2017, after which monthly sampling continued through May 2019. At each sampling, three bushels of oysters and associated cultch were randomly collected using a standard commercial oyster dredge. Up to 100 live animals, availability permitting, and associated boxes were measured (maximum length). Minimally 20 oysters (if present) representative of the range of sizes encompassing the size–frequency distribution were retained, and the cultch was weighed (lbs).

The retained oysters from the Pass Christian Reef were scrubbed and the shell lengths (maximum dimension from

hinge to bill) remeasured (mm). The oysters were shucked and patted dry before weighing both valves to generate a total shell weight (g) for each individual. A live oyster shell length-to-weight relationship was established using the allometric equation:

$$W = aL^b,\tag{1}$$

where W is the shell weight (g), a is an allometric coefficient, L is the shell length (mm), and b is a scaling exponent. A standard OLS regression (R version 3.6.0) was fit to the log-transformed data to estimate the allometric parameters. As the bulk of oysters that were measured had shell lengths between 60 and 115 mm, only animals within this length range were included.

In April 2019, one bushel of cultch was retained from the monthly sampling event. The shells were scrubbed and left to dry in the sun for one day. Whole valves and major fragments (shells whole enough to obtain an accurate length measurement—see Davies et al. 1990) were culled from the bushel. Henceforth, these valves and major fragments will be referred to as dead shell. Each valve was denoted as a right or left valve, and the length, width, and weight of each valve were measured. The ratio of the number of left valves to the number of right valves was obtained. The remaining minor shell fragments (valves sufficiently damaged or degraded such that a length measurement was not possible) were identified as right or left valves where possible.

In May 2019, three bushels of oysters and associated cultch were collected from the Pass Christian Reef and a nearby reef, Henderson Point, where live adult oysters were still relatively abundant compared with the limited live oysters at Pass Christian. Live oysters were culled from the samples and sorted into 10-mm-size bins. Five oysters per size class (if present) were processed using the same methods as the 2016 collection; however, the left and right valves were measured and weighed individually. The shells were then left to dry in the sun for one day, after which the valves were weighed once more to determine whether a weight differential existed between wet (oysters that had been scrubbed and immediately patted dry for processing) and dry oyster valves. A paired t-test was used to determine whether the means of the wet and dry valve weights differed significantly. The weight ratio of the left:right valves for live oysters was obtained for each reef.

The bushel of dead shell collected from Pass Christian in April 2019 contained only disarticulated, single valves, whereas both valves of each oyster were weighed together in 2016. To compensate for this, the weight ratio of the left (P_L) to right (P_R) valves generated from the 2019 Henderson Point collection was used to estimate the total shell weight of each oyster from just one valve in the April 2019 dead assemblage. Henderson Point oysters were used because too few live oysters were present on the Pass Christian Reef in 2019 to support the analysis. Articulated shell weights for the April 2019 Pass Christian dead shell collection were then obtained using the corresponding valve weight ratio. These total shell weights were used to generate a shell length:weight relationship for the dead shell using the same methods as the 2016 collection. Statistical comparisons to test the effect of length and collection year on shell weight were made using ANCOVA on log-transformed length and weight data (R version 3.6.0).

Calculating Total Carbonate Loss

To calculate the total amount of carbonate lost over the course of the experiment, population length–frequency distributions were established. This was performed in two ways: the first was the length–frequency distribution from the last collection of live oysters before the September 2016 mortality event, and the second was the length–frequency distribution of the 2019 dead shell. Each of the two distributions was standardized to 100 animals to generate the number of animals within each 1-mm increment from 60 to 115 mm. The resulting size frequencies differed as might be anticipated from separate samples taken several years apart on any oyster bed as the patchiness of oysters on oyster beds is well described (Powell et al. 1987, Fegley et al. 2003, Powell et al. 2017). Consequently, the allometric parameters for each of the collections were used to calculate a shell weight for each shell length, and this was multiplied by the number of animals within each 1-mm increment. These two length–frequency estimates were used in parallel in the following series of calculations under the assumption that they were independent estimates of the original size frequency in the population, providing the amount of carbonate initially present in August 2016 as well as two estimates of shell loss.

The number of grams of carbonate that valves lost (T_{CL}) over the 2.67-y period between collections was calculated for each of the two distributions:

$$T_{CL} = \sum_{i=60}^{115} n_i(W_{L_i} - W_{D_i}),\tag{2}$$

where W_L is the shell weight of the 2016 oysters, W_D is the weight of the 2019 dead shell, and n_i is the number of shells in each mm interval.

As both valves were weighed together in the 2016 collection, the individual weights of the left and right valves are unknown. To address this issue, the total weight (g) of right valves for the 2016 oysters (W_{RV}) was obtained as

$$W_{RV} = W_L \times P_R,\tag{3}$$

where P_R is the proportion of weight occupied by right valves in the live assemblage from Henderson Point from 2019.

To quantify whether left and right valves were equally represented in the 2019 dead assemblage, the ratio of left (P_{NL}) to right (P_{NR}) valves was determined. Significantly more left valves were present in the dead assemblage, so the proportion of right valves that had presumably deteriorated to a point that they were not retained by the dredge (P_G) in the time elapsed between collections was determined.

W_M, the amount of carbonate (g) not present in the dead assemblage due to a loss of whole right valves and right-valve major fragments between 2016 and 2019, was obtained as the total weight of the right valves (W_{RV}) multiplied by the proportion of right valves not retained by the dredge (P_G):

$$W_M = W_{RV} \times P_G.\tag{4}$$

The total amount of carbonate (g) lost between 2016 and 2019, T, was then calculated as

$$T = T_{CL} + W_M.\tag{5}$$

Using the total amount of carbonate lost from the reef over the course of the study, λ, the shell loss rate, can be calculated:

$$\lambda = \frac{-\ln\left(\frac{W_L - T}{W_L}\right)}{t}, \qquad (6)$$

where t is the elapsed time in years between the live shell collection and the dead shell collection, 2.67 in this case. Then, the half-life, $t_{1/2}$, for shell on the reef is:

$$t_{1/2} = -\ln(0.5)/\lambda. \qquad (7)$$

These calculations yield two estimates of the total amount of carbonate lost from the reef and corresponding half-life estimates based on the 2016 and 2019 length–frequency distributions, assuming that each length–frequency distribution is an independent measure of the original size–frequency distribution in August 2016. An alternative view is that the two length–frequency distributions differ as a consequence of differential preservation of size classes, a view that has precedent from other taphonomic studies (Cummins et al. 1986). In this view, the significant differential between the two length frequencies is the differential contribution of animals 60–69 mm. For the population length frequency to shift from the distribution observed in 2016 to that of 2019, 65.59% of the animals in the 60- to 69-mm size class were lost by 2019. To calculate the weight of the valves that disappeared from this size class, T_M, the weight of all animals or valves between 60 and 69 mm was summed using the 2016 size–frequency distribution and multiplied by 0.6559. T_M was then added to the total carbonate loss (T) estimate to get T_{MAX}, the maximum carbonate loss estimate, based on the 2016 size frequency. The T_{MAX} estimate was then used in Eqs. 6, 7 to calculate a half-life. Thus, three estimates of the amount of carbonate lost from the reef (g) and three half-life estimates for oysters in the Mississippi Sound were obtained by this study.

RESULTS

The analysis is made possible by the nearly complete recruitment failure on the Pass Christian Reef over the 2017 to 2018 period. The number of juvenile oysters (25–50 mm shell length) per gram of carbonate is displayed in Figure 1. Results demonstrate that little recruitment occurred following the 2016 mortality event at the Pass Christian Reef, whereas three nearby reefs exhibited an increase in the number of juvenile oysters beginning
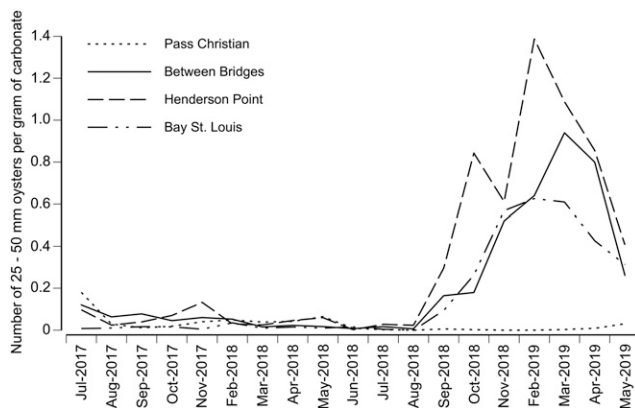
in August 2018. Recruitment failure on the Pass Christian Reef ensures that limited carbonate addition occurred between the mortality event in 2016 and the collection of dead shell in 2019.

Carbonate Loss Estimates, Shell Present in 2019

In August 2016, live oysters comprised 89% of the total carbonate in the sample, with the remainder being cultch and boxes, most of which was cultch (Fig. 2). The limited presence of cultch in the dredge tows suggests that the recovery of old buried shell was minimal. Few animals recruited during the intervening period between August 2016 and April 2019. By September 2016, no live oysters were present, and a substantial increase in boxes (dead, articulated valves) was observed. As the proportion of boxes decreased over time as disarticulation occurred, the proportion of cultch increased. Thus, the vast majority of intact valves collected in April and May 2019 originated from the death of oysters in September 2016.

The allometric parameters for the 2016 and 2019 collections are shown in Table 1. The 2019 dead shell, having been exposed to taphonomic processes for over 2 y, was lighter for a given length, compared with the 2016 oysters (Fig. 3). Results of the ANCOVA analysis indicated that the interaction term was not significant (Table 2); thus, it was removed, and the model was refit (Table 3). Length had a highly significant effect on shell weight, as expected ($P < 2e^{-16}$). The collection year also had a significant effect on shell weight ($P = 0.0166$), as suggested by the lower scaling exponent for the dead shell collected in 2019.

Significant differences were found between the weights of wet (blotted dry) and air-dried Henderson Point valves ($P = 3.43e^{-15}$), with a mean shell weight differential of 3.55%. Left valves weighed more than right valves. Based on the total shell weight for valves measured from Henderson Point, the proportion of the total weight contributed by left valves (P_L) was 0.5629.

The length–frequency distributions from August 2016, the last collection in which live oysters were present before the 2016 mortality event, and from the 2019 dead shell differed (Fig. 4), with the most substantive difference being the differential in contribution of valves in the 60- to 69-mm size class. Fewer valves in that smaller size class were found in the 2019 sample.

The total shell weight of live oysters (W_L) generated for each length–frequency distribution and the shell weight of whole

Figure 1. Number of recently recruited (25- to 50-mm shell length) oysters per gram of carbonate for the four reefs.
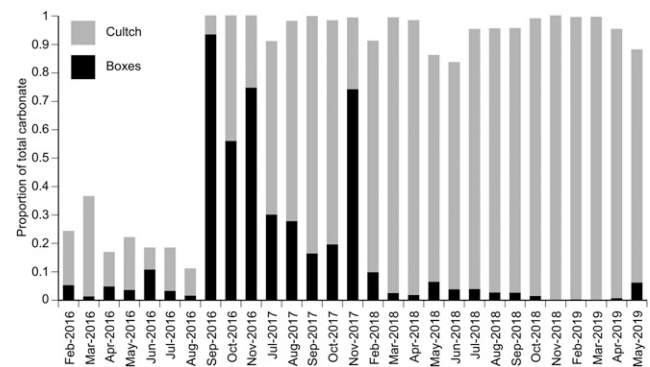

Figure 2. Proportion of total carbonate due to cultch (gray) and boxes (black) at Pass Christian. The differential on the y-axis between 1.0 and the top of the gray box indicates the proportion of carbonate present in the form of live animals.

TABLE 1.

Allometric parameter estimates for the 2016 and 2019 collections relating shell weight (g) to shell length (mm).

	a	*b*
2016 live shell	0.00227	2.4017
2019 dead shell	0.01507	1.9471

Analysis was conducted only on animals with shell lengths 60–115 mm.

valves and major fragments (W_D) was used to estimate the amount of carbonate lost over the intervening 2.67 y between August 2016 and April 2019 (Table 4). Estimates were based on the 2016 and 2019 size–frequency distributions as both might be fair representations of the original size frequency of live animals before the mass mortality event. Carbonate loss (T_{CL}) was estimated as 8.3% based on the 2016 distribution and 11.2% based on the 2019 distribution.

Carbonate Loss from Missing Right Valves

A striking differential exists between the numbers of left and right valves that were present in the 2019 samples. The ratio of the number of left to right valves in the 2019 dead shell ($P_{NL} = 0.67$, $P_{NR} = 0.33$) differed substantially from the 50:50 expectation because live oysters have a corresponding left and right valve ($P < 0.00001$, $n = 158$; binomial test). The left:right ratio of 67:33 indicates that 50% of the right valves were missing from the sample or fragmented to a point of being unidentifiable as right or left valves, thus $P_G = 0.5$. Further evidence that more right valves were missing from the dead assemblage was observed in the corresponding ratio obtained from the minor fragments that remained identifiable as left or right valves. Of the identifiable minor fragments, 85% were left valves and 15% were right valves. This ratio differed from the expected 50:50 ratio of live animals ($P < 0.00001$, $n = 162$; binomial test) and also significantly from the whole + major fragment ratio of 67:33 ($P < 0.00001$, $n = 162$; binomial test).

TABLE 2.

ANCOVA results using log-transformed length and weight data for live animals from 2016 and dead shell from 2019 including the interaction term.

	Df	Sum sq	*F* value	Pr(>*F*)
Length	1	3.6106	144.2125	<2e-16
Year	1	0.0570	2.2775	0.1325
Length:year	1	0.0638	2.5474	0.1117
Residuals	266	6.6598	–	–

The 50% loss of right valves was incorporated as a minimal estimate of carbonate loss of this type, recognizing that the process of biased right-valve loss is significantly farther advanced for the minor fragments. Estimates of carbonate loss derived thereby using each of the two length–frequency distributions are shown in Table 4. The two estimated total carbonate losses, T, between 2016 and 2019 were 1,978.30 and 2,920.05 g. These results suggest that between 30% and 33% of carbonate present in the living assemblage (W_L) in August 2016 was lost by April 2019. Based on these bulk carbonate loss estimates, the Pass Christian oyster shells have a half-life $(t_{1/2})$ between 4.6 and 5.1 y. Given the additional bias in left:right valve ratios in the minor fragments, these estimates probably represent upper bounds of the true half-life of oyster shell on the Pass Christian Reef.

These half-life estimates may be conservative, as they do not include the amount of carbonate that would need to be lost to explain the change in length–frequency distribution observed between 2016 and 2019. Determining an additional loss term rests on the assumption that the two length frequencies are not merely two estimates of the 2016 size frequency of live animals. Incorporating an additional loss in the estimate of the half-life of shell must, therefore, be carried out under this proviso. Incorporating the 65.59% loss of animals in the 60- to 69-mm size class yields a maximum carbonate loss (T_{MAX}) of 3,339.05 g, suggesting 51% of the carbonate added to the reef in August 2016 was lost by April 2019. The estimated shell half-life falls to 2.6 y.

DISCUSSION

Characteristics of the Taphonomic Process

The mass mortality event that took place in the western Mississippi Sound in 2016 provided a unique opportunity to investigate the rate of taphonomic degradation of oyster shells. Although many oyster reefs in the region were severely impacted by the mortality event, the populations of a majority of the reefs exhibited a modest recovery within 2 y (Fig. 1). By
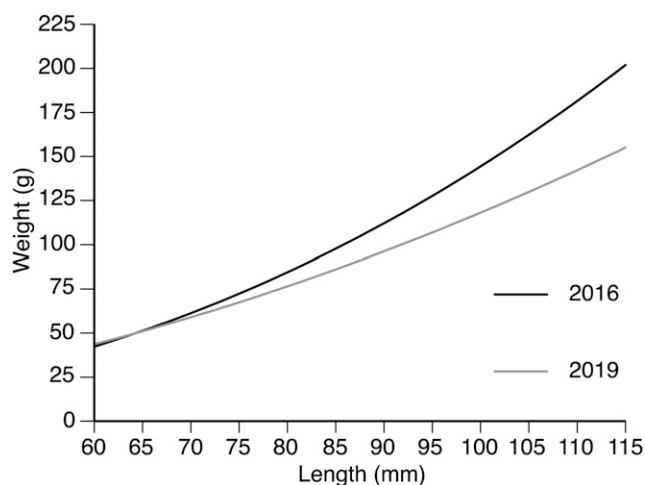

Figure 3. Length:weight relationship for 2016 oysters and 2019 dead shell from the Pass Christian Reef. One hundred twenty six valves were measured in 2016, and 144 valves were measured in 2019.

TABLE 3.

ANCOVA results using log-transformed length and weight data for live animals from 2016 and dead shell from 2019.

	Df	Sum sq	*F* value	Pr(>*F*)
Length	1	5.8097	230.7107	<2e-16
Year	1	0.1462	5.8077	0.01663
Residuals	267	6.7236	–	–
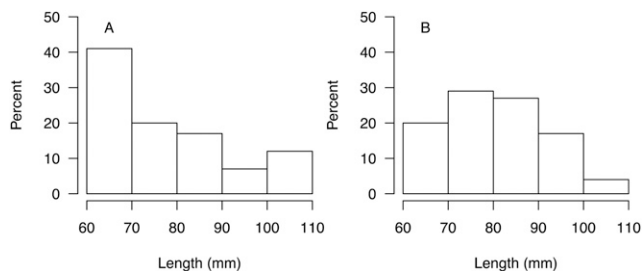
Figure 4. Length–frequency distributions for the left valves of the live animals from (A) August 2016 and (B) April 2019 dead shell. Distributions were standardized to 100 animals based on 38 live measurements from 2016 and 97 left-valve measurements from 2019.

contrast, at the Pass Christian Reef, limited recruitment occurred in the following years, and the abundance of live oysters remained very low so that little shell addition occurred over a 2.67-y period following the mortality event. This permitted a direct comparison between shell present as living oysters in August 2016 and dead shell collected in April 2019 that had been exposed to taphonomic processes for over 2 y.

Perhaps unsurprisingly, shell weights in the 2019 dead shell were lighter for a given shell length (Fig. 3). Whereas it is predictable that shell length has a significant effect on shell weight, ANCOVA results show that time since death also significantly impacted shell weight. A visual examination of the condition of the valves from the 2019 dead shell sheds light on why the 2016 and 2019 length:weight relationships differ. Figure 5 displays valves from the April 2019 dead shell collection from Pass Christian. Most valves were riddled with holes, some of which perforated the valves. Deterioration of the shell surface, whether by dissolution, maceration, or abrasion, was ubiquitous, and edge erosion was commonplace. Figure 6 displays valves from the dead shell on Pass Christian collected in November 2017; these valves have fewer holes and exhibit much less degradation than those of 2019 (Fig. 5). Shell-boring organisms such as the clionid sponge *Cliona celata* and the spionid polychaete *Polydora* sp. are known to cause extensive damage to oyster shells, increasing the rate of chemical dissolution as well as that of other taphonomic processes such as fragmentation (Blake & Evans 1973, Powell & Davies 1990, Carver et al. 2010, Powell et al. 2011, Carroll et al. 2015). Although unconfirmed beyond visual inspection, most of the shell voids observed likely were the products of sponge and polychaete boring. Edge erosion is more likely the result of physical abrasion and biological manipulation of shells after death. During the intervening 2.67 y, effectively all boxes produced late in

August 2016 disarticulated (our unpubl. data), giving further evidence of the effectiveness of biological degradation and shell movement, by physical or biological means, after death. In addition, fouling microorganisms such as bacterial and fungal biofilms can break down the organic matrix of the shell, exposing crystallites to chemical attack and creating microscopic pits within the surficial calcite, which can enhance dissolution by creating additional surface area (Glover & Kidwell 1993, Morse et al. 2007), as dissolution rates of exposed shell are controlled at least in part by the available surface area (Kosnik et al. 2009, Subhas et al. 2015).

Caveats in the Estimation of Shell Half-Life

The length–frequency distributions in Figure 4 show a clear disparity in the contribution of valves in the 60- to 69-mm size class, with a larger proportion of animals of this size collected in 2016. The apparent shift in the length–frequency distribution from 2016 to 2019 could potentially be a sampling issue as the length–frequency distributions were based on only one bulk sample from three dredge hauls on the reef in each year. Alternatively, these distributions may accurately represent the true population distributions which would support the notion that smaller valves do in fact succumb to taphonomic processes faster than larger valves, as discussed subsequently. If the population truly lost two-thirds of the valves initially present in this size class because of taphonomic processes, then basing the amount of carbonate loss only on the weight differential between 2016 and 2019 and the missing right valves would be an underestimate. As a consequence, estimates of shell loss are provided disregarding and including this potential shell loss.

The extensive boring observed in the 2019 dead shell compromises the structural integrity of the valve, likely resulting in increased fragmentation (Young & Nelson 1985). One possibility is that previously intact valves may break down during the collection process, leading to an increase in the number of smaller shells potentially selected against by the dredge. Such events bias the number of intact valves and their size frequency, which might lead to a biased estimate of shell loss. Although the dredging process can be expected to insert some degree of bias, a number of observations suggest that the bias is limited. Powell et al. (2001) in a focused evaluation of an intensive dredging process did not detect an increase in disarticulation of articulated valves (boxes) and found only occasional minor chipping on intact valves of live oysters. In addition, the Pass Christian Reef was not fished over the time frame of the study so that the only dredging conducted accrued from our sampling program, thereby minimizing the accrual of

TABLE 4.

Results of the carbonate loss calculations based on each of the respective 2016 and 2019 length–frequency distributions.

	W_L (g)	T_{CL}	W_{RV} (g)	W_M (g)	T (g)	$t_{1/2}$	T_M (g)	T_{MAX} (g)	$t_{1/2}$
2016	6,552.55	546.24	2,864.12	1,432.06	1,978.30	5.149	1,360.75	3,339.05	2.598
2019	8,838.96	988.29	3,863.51	1,931.75	2,920.05	4.615	–	–	–

W_L, shell weight of the 2016 oysters; T_{CL}, number of grams of carbonate valves lost between collections; W_{RV}, total weight (g) of right valves for the 2016 oysters; W_M, the amount of carbonate (g) not present in the dead assemblage because of a loss of whole right valves and major fragments; T, the total amount of carbonate (g) lost between 2016 and 2019; $t_{1/2}$, half-life; T_M, weight of the valves that disappeared from this 60- to 69-mm size class; T_{MAX}, the maximum carbonate loss estimate.

Figure 5. Dead shell collected from the Pass Christian Reef in April 2019.

any dredge-associated fragmentation. Notably, Powell and Ashton-Alcox (2004) and Ashton-Alcox et al. (2013) observed that dredges select against smaller shells in the early part of the towing process, as expected, but that clogging of the dredge minimizes this effect. Dredge efficiencies tend to decline modestly on unfished reefs for reasons that are not fully explained (Powell & Ashton-Alcox 2004, 2013), and that effect might be anticipated in this study; this might limit clogging and reduce retention of minor fragments but is unlikely to increase fragmentation. Finally, major fragments were included in the analysis, and minor fragments were tracked to the extent feasible, thereby including to the degree possible any fragments that might have been produced by the sampling process. Thus, the act of sampling is an unlikely source of shell loss beyond the influence of size selectivity.

The bias of size selectivity can be anticipated; for this reason, this study focused on whole shells and major fragments 60 mm and larger. This larger fraction contributes the bulk of the carbonate weight on a reef and represents the fraction most likely to survive taphonomic attack (Cummins et al. 1986, Mann et al. 2009b). In fact, the principal concern revealed in this study is not size selectivity *per se* but the increased differential in left-right valve ratios for minor fragments as opposed to major fragments and whole shells. This preferential retention of left valves strongly suggests that the estimate of shell half-life represents an upper bound as a very large fraction of right valves was lost between 2016 and 2019. The dredge efficiency for cultch capture is significantly less than that of live animals and boxes (Powell et al. 2002, 2007, Mann et al. 2004), an effect that likely accrues from the lower selectivity for minor fragments, which may in part explain

the differential left:right valve ratios, but which, if so, would nonetheless indicate a rapid degradation rate for right valves. Regardless, our analysis was unable to include minor fragments in the estimate of shell half-life, and this introduces an unknown bias which likely produces an overestimate of shell half-life.

The 2016 live oyster weights were generated by weighing both valves, whereas the 2019 weights for the dead shell perforce were limited to only one valve as all dead oysters had disarticulated over the time period between collections. As left valves tend to be heavier than right valves, simply halving the weight of paired valves to generate a total shell weight is not appropriate. Thus, a weight ratio between left and right valves was developed to more accurately estimate the total shell weight from a single valve. The weight ratio could not be generated retroactively from the 2016 dataset; thus, live animals collected from Henderson Point in 2019 were used for this analysis. Henderson Point was chosen because these valves were more representative of the condition of the live animals from Pass Christian in 2016 in terms of limited surficial boring by epibionts than the few live oysters collected from Pass Christian in 2019 (Fig. 7). The size frequency of the Henderson Point oysters also more accurately resembled the size frequencies observed in the 2016 Pass Christian collections (Fig. 8). Nonetheless, some

Figure 6. Dead shell collected from Pass Christian in 2017.
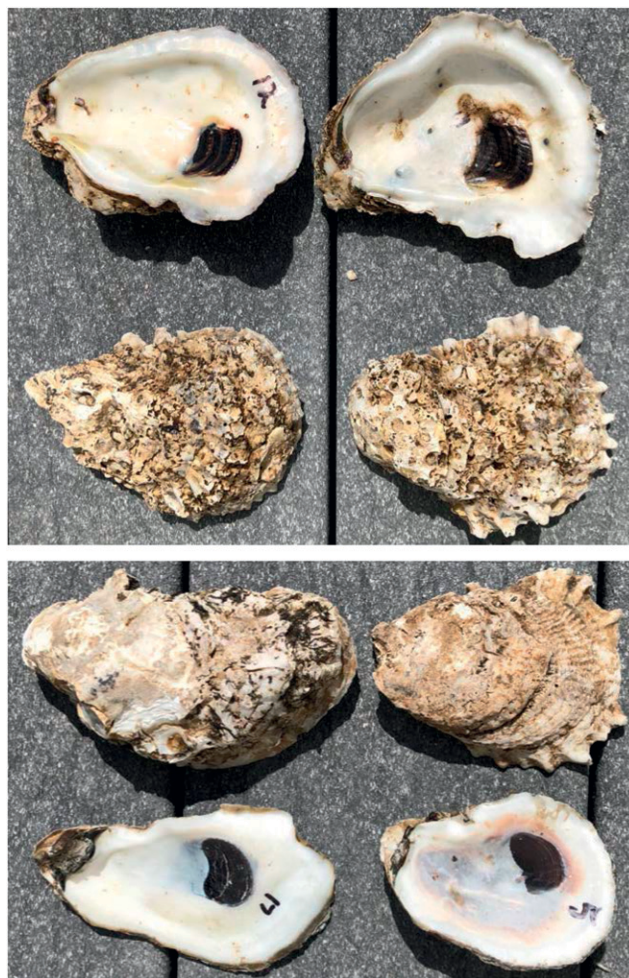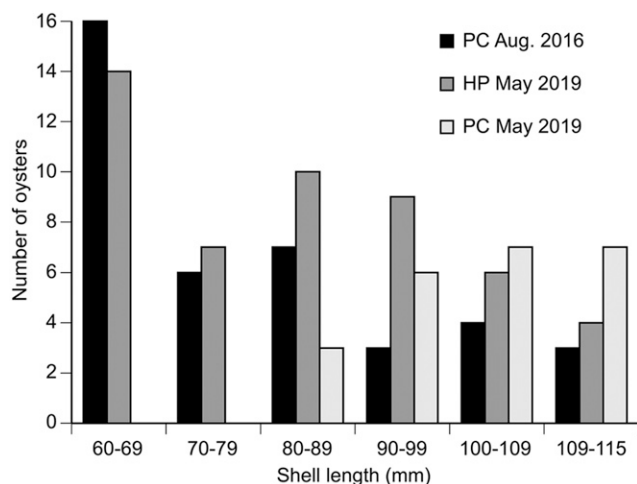
Figure 7. Top: shells from live oysters collected from Pass Christian in 2019. Bottom: shells from live oysters collected from Henderson Point in 2019.

Figure 8. Size frequency of live oysters from Pass Christian (PC) in August 2016 (black) and May 2019 (light gray), and live oysters from Henderson Point (HP) in May 2019 (dark gray).

bias likely resulted from the absence of single valve weights from the 2016 dataset.

Another uncertainty in the comparison of the 2016 live versus 2019 dead shell weights arises from the fact that oysters processed in 2016 were blotted dry before weighing, whereas the 2019 dead shell was air-dried. Although live oysters do not have holes completely bored through the valves as seen in the dead shell collection, valves are sufficiently porous that a significant difference in shell weight may exist between a valve that has been blotted dry and a valve that has been air-dried. Direct comparison showed, however, that the weight differential was small in comparison with the weight of shell lost through taphonomic degradation.

Finally, all length measurements in 2016 were in fact left-valve measurements, as the lengths were recorded before the shucking of each individual. Although in some cases the left and right valves can be of the same length, left valves are typically longer than right valves. Based on the length measurements from the live collections from Pass Christian and Henderson Point in 2019, right valves were on average 91% of the length of left valves. The largest observed differential between two corresponding valves was 22 mm, with at least a 10-mm differential in 51% of the left–right valve length comparisons. Consequently, to the extent possible, estimates of shell loss were carried out independently for right and left valves, and size–frequency differentials were based on histograms for left valves.

The Conundrum of Unequal Valves

Generally, larger more robust shells should be preferentially preserved in taphonomically rigorous environments (Cummins et al. 1986, Tomašových 2004). Right valves, then, would be expected to degrade faster than the left valves, particularly in cases where a very large length and weight difference exists, which is commonplace, as left valves contribute on average about 56% of the total shell weight for each oyster. Moreover, oysters, being reef builders, attach to other substrates *via* the lower or left valve. This valve is thus more protected from boring organisms and dissolution than the fully exposed right

valve while the oyster is alive. Furthermore, on many reefs including Pass Christian, oysters form clumps that persist even after death. Although boxes eventually disarticulate, undisturbed aggregates of left valves can remain intact, whereas the right valves detach and presumably fall off, which likely makes right valves more susceptible to physical disturbances and fragmentation. This biased preservation of oyster left valves has existed since at least the Cretaceous (Tapanila et al. 2015).

Despite these intuitive facts, the disparity between the number of left and right valves present in the dead shell collection is surprising, with left valves comprising 67% of the intact valves and 85% of the minor fragments. This suggests that in the time between collections, minimally 50% of the right valves originally present on the reef have disappeared and that the differential rate of degradation between left and right valves continues apace as the valves degrade so that minor fragments are overwhelmingly represented by left valves. The missing right valves may have been too fragmented to be collected using a standard commercial dredge, but the fact that only 15% of the identifiable minor fragments were right valves strongly implies that the missing right valves are in fact gone and not simply absent as a product of biased sampling.

The Half-Life and Implications for Management

Summing the amount of carbonate lost between the live and dead valve weights and adding a conservative estimate of the number of right valves lost, 50%, produces an estimate that 30%–33% of the total carbonate present on the reef in 2016 and added to the shell bed by the mass mortality event was lost by 2019. This suggests that a conservative estimate of the half-life of oyster shell in the Mississippi Sound is between 4.6 and 5.1 y. Including all of the valves that had to be lost in the 60- to 69-mm size class, if the differential in length frequencies is due to valve loss, yields a maximum carbonate loss of 51%, suggesting the half-life may be as low as 2.6 y.

A number of half-life estimates for oyster shell have been reported. Some of these come from time series data relating the addition of boxes to the shell bed through mortality to the quantity of shell present, from which the loss rate can be derived (Powell et al. 2006, Mann et al. 2009a). Others are derived from laboratory experiments (Waldbusser et al. 2011, Ries et al. 2016). These estimates generally agree in setting a half-life in the range of 2–10 y, a surprisingly short time in comparison with the preservability of most bivalve shells exclusive of mussels (e.g., Callender et al. 1994; Powell et al. 2011, see also Harzhauser et al. 2016). An in-field natural experiment in which added shell was directly followed over time has not been carried out for oyster shell; however, the Pass Christian mortality event provided this opportunity. The results of that opportunity are reported here, and the half-life estimates fall precisely within the range of the previous less direct estimates. Oyster shell degrades rapidly with a half-life well below 10 y in most cases. The case histories now include a wide latitudinal range and a wide temperature range, suggesting that these rapid shell degradation rates are the norm over most of the range of the eastern oyster.

The evolution of sustainable management for oyster fisheries and oyster reefs has been toward the combining of stock and cultch management initially recommended by Powell and Klinck (2007) and Mann and Powell (2008), and furthered in the development and implementation of a number of models

directed at the simultaneous need to retain fishable oyster stock and sufficient cultch to promote recruitment (Soniat et al. 2012, 2014, 2019, see also Powell et al. 2018). The short half-life of oyster shell emphasizes the fragility of the oyster reef system to overfishing, as insufficient shell addition to balance shell loss ineluctably will lead to reef degradation, recruitment constraint, and eventually not only to stock collapse but also to the loss of reef structure (Powell et al. 2012a). This study reemphasizes the necessity of cultch management by documenting in a different way and in a different locale similarly rapid rates of shell destruction. The removal of oyster shell through harvest must be managed extremely conservatively (Powell et al. 2012a, 2018); otherwise, the reef itself will disappear.

Oyster bed restoration and enhancement programs often rely on the addition of carbonate to estuarine sediments (Bushek et al. 2004, Mann & Powell 2008, Kennedy et al. 2011, Harding et al. 2012, Ishikawa & Kennedy 2014). These programs rarely evaluate the potential for long-term success in terms of the prospective rate of shell addition and loss. Measured half-lives for oyster shell necessitate that restored areas recruit successfully and predictably to perpetuate the shell bed or that continued shell addition occur. Single shell-planting events without long-term recruitment potential will produce only transient results as shell half-lives are on the order of only two to three times the anticipated life span of the initial recruits in all but the lowest salinity reaches of the estuary (Kraeuter et al. 2007, Paynter et al. 2010), even if fishing is prohibited. Limestone is often used as an alternative to oyster shell (Soniat & Burton 2005, La Peyre et al. 2014, Kuykendall et al. 2015). Given the sensitivity of calcium carbonate of any form to destruction in the marine world (Arvidson et al. 2003, Hu & Burdige 2008, Waldbusser & Salisbury 2014), an estimate of the half-life of limestone in cultch plants is sorely needed.

LITERATURE CITED

Arvidson, R. S., I. E. Ertan, J. E. Amonette & A. Lutige. 2003. Variation in calcite dissolution rates: a fundamental problem? *Geochim. Cosmochim. Acta* 67:1623–1634.

Ashton-Alcox, K. A., E. N. Powell, J. A. Hearon, C. S. Tomlin & R. M. Babb. 2013. Transplant monitoring for the New Jersey Delaware Bay oyster fishery. *J. Shellfish Res.* 32:459–469.

Beck, M. W., R. D. Brumbaugh, L. Airoldi, A. Carranza, L. D. Coen, C. Crawford, O. Defeo, G. J. Edgar, B. Hancock, M. Kay, H. Lenihan, M. W. Luckenbach, C. L. Toropova & G. Zhang. 2009. Shellfish reefs at risk a global analysis of problems and solutions. Arlington, VA: The Nature Conservancy. 52 pp.

Best, M. M. R. 2008. Contrast in preservation of bivalve death assemblages in siliciclastic and carbonate tropical shelf settings. *Palaios* 23:796–809.

Best, M. M. R. & S. M. Kidwell. 2000. Bivalve taphonomy in tropical mixed miliciclastic-carbonate settings. I. Environmental variation in shell condition. *Paleobiology* 26:80–102.

Best, M. M. R., T. C. W. Ku, S. M. Kidwell & L. M. Walter. 2007. Carbonate preservation in shallow marine environments: unexpected role of tropical siliciclastics. *J. Geol.* 115:437–456.

Beukema, J. J. 1980. Calcimass and carbonate production by molluscs on the tidal flats in the Dutch Wadden Sea: I. the tellinid bivalve *Macoma balthica*. *Neth. J. Sea Res.* 14:323–338.

Blake, J. & J. Evans. 1973. Polydora and related genera (Polychaeta: Spionidae) as borers in mollusk shells and other calcareous substrates. *Veliger* 15:235–249.

Bottjer, D. J. & J. G. Carter. 1980. Functional and phylogenetic significance of projecting periostracal structures in the Bivalvia (Mollusca). *J. Paleontol.* 54:200–216.

Bushek, D., D. Richardson, M. Y. Bobo & L. D. Coen. 2004. Quarantine of oyster shell cultch reduces the abundance of *Perkinsus marinus*. *J. Shellfish Res.* 23:369–373.

Cai, W.-J., F. Chen, E. N. Powell, S. E. Walker, K. M. Parsons-Hubbard, G. M. Staff, Y. Wang, K. A. Ashton-Alcox, W. R. Callender & C. E. Brett. 2006. Preferential dissolution of carbonate shells driven by petroleum seep activity in the Gulf of Mexico. *Earth Planet. Sci. Lett.* 248:227–243.

Callender, R. & E. N. Powell. 2000. Long-term history of chemoautotrophic clam-dominated faunas of petroleum seeps in the northwestern Gulf of Mexico. *Facies* 43:177–204.

Callender, W. R., E. N. Powell & G. M. Staff. 1994. Taphonomic rates of molluscan shells placed in autochthonous assemblages on the Louisiana continental slope. *Palaios* 9:60–73.

Carriker, M. R., R. E. Palmer & R. S. Prezant. 1980. Functional ultramorphology of the dissoconch valves of the oyster *Crassostrea virginica*. *Proc. Natl. Shellfish. Assoc.* 70:139–183.

Carroll, J. M., K. A. O'Shaughnessy, G. A. Diedrich & C. M. Finelli. 2015. Are oysters being bored to death? Influence of *Cliona celata* on *Crassostrea virginica* condition, growth and survival. *Dis. Aquat. Organ.* 117:31–44.

Carver, C. E., I. Thériault & A. L. Mallet. 2010. Infection of cultured eastern oysters *Crassostrea virginica* by the boring sponge *Cliona celata*, with emphasis on sponge life history and mitigation strategies. *J. Shellfish Res.* 29:905–915.

Chinzei, K. 2013. Adaptation of oysters to life on soft substrates. *Hist. Biol.* 25:223–231.

Coen, L. D., R. D. Brumbaugh, D. Bushek, R. Grizzle, M. W. Luckenbach, M. H. Posey, S. P. Powers & S. G. Tolley. 2007. As we see it. Ecosystem services related to oyster restoration. *Mar. Ecol. Prog. Ser.* 341:303–307.

Cummins, H., E. N. Powell, R. J. Stanton & G. Staff. 1986. The size-frequency distribution in palaeoecology: effects of taphonomic processes during formation of molluscan death assemblages in Texas bays. *Palaeontology* 29:495–518.

Darrow, E. S., R. H. Carmichael, C. F. T. Andrus & H. E. Jackson. 2017. From middens to modern estuaries, oyster shells sequester source-specific nitrogen. *Geochim. Cosmochim. Acta* 202:39–56.

Davies, D. J., E. N. Powell & R. J. Stanton. 1989. Relative rates of shell dissolution and net sediment accumulation - a commentary: can shell beds form by the gradual accumulation of biogenic debris on the sea floor? *Lethaia* 22:207–212.

Davies, D. J., G. M. Staff, W. R. Callender & E. N. Powell. 1990. Description of a quantitative approach to taphonomy and taphofacies analysis: all dead things are not created equal. In: Miller III, W., editor. Paleocommunity temporal dynamics: the long-term development of multispecies assemblages. *Spec. Publ. (Paleontol. Soc.)* 5:328–350.

Diez, M. E., J. M. Orensanz, F. Márquez & F. Cremonte. 2013. Shell damage in the Tehuelche scallop *Aequipecten tehuelchus* caused by

Polydora rickettsi (Polychaeta: Spionidae) infestation. *J. Invertebr. Pathol.* 114:107–113.

Edinger, E. N. & O. A. Sherwood. 2012. Applied taphonomy of gorgonian and antipatharian corals in Atlantic Canada: experimental decay rates, field observations, and implications for assessing fisheries damage to deep-sea coral habitats. Neues Jahrbuch Geol. Palaontol. Abhand. 265:199–218.

Eleuterius, C. K. 1977. Location of the Mississippi Sound oyster reefs as related to salinity of bottom waters during 1973–1975. *Gulf Res. Rep.* 6:17–23.

Elner, R. W. & R. E. Lavoie. 1983. Predation on American oysters (*Crassostrea virginica* (Gmelin)) by American lobsters (*Homarus americanus* (Milne-Edwards)), rock crabs (*Cancer irroratus* (Say)), and mud crabs (*Neopanope sayi* (Smith)). *J. Shellfish Res.* 3:129–134.

Esteban-Delgado, F. J., E. M. Harper, A. G. Checa & A. B. Rodríguez-Navarro. 2008. Origin and expansion of foliated microstructure in pteriomorph bivalves. *Biol. Bull.* 214:153–165.

Fegley, S. R., S. E. Ford, J. N. Kraeuter & H. H. Haskin. 2003. The persistence of New Jersey's oyster seedbeds in the presence of oyster disease and harvest: the role of management. *J. Shellfish Res.* 22:451–464.

Foote, M., J. S. Crampton, A. G. Beu & C. S. Nelson. 2015. Aragonite bias, and lack of bias, in the fossil record: lithological, environmental, and ecological controls. *Paleobiology* 41:245–265.

Glover, C. P. & S. M. Kidwell. 1993. Influence of organic matrix on the post-mortem destruction of molluscan shells. *J. Geol.* 101:729–747.

Grabowski, J. H., R. D. Brumbaugh, R. F. Conrad, A. G. Keeler, J. J. Opuluch, C. H. Peterson, M. F. Piehler, S. P. Powers & A. R. Smith. 2012. Economic valuation of ecosystem services provided by oyster reefs. *Bioscience* 62:900–909.

Green, M. A., R. C. Aller & J. Y. Aller. 1998. Influence of carbonate dissolution on survival of shell-bearing meiobenthos in nearshore sediments. *Limnol. Oceanogr.* 43:8–28.

Green, M. A., M. E. Jones, C. L. Boudreau, R. L. Moore & B. A. Westman. 2004. Dissolution mortality of juvenile bivalves in coastal marine deposits. *Limnol. Oceanogr.* 49:727–734.

Guay, M. & J. H. Himmelman. 2004. Would adding scallop shells (*Chlamys islandica*) to the sea bottom enhance recruitment of commercial species? *J. Exp. Mar. Biol. Ecol.* 312:299–317.

Gunter, G., C. E. Dawson & W. J. Demoran. 1957. Determination of how long oysters have been dead by studies of their shells. *Proc. Natl. Shellfish. Assoc.* 47:31–33.

Gutiérrez, J. L., C. G. Jones, D. L. Strayer & O. O. Iribarne. 2003. Mollusks as ecosystem engineers: the tole of shell production in aquatic habitats. *Oikos* 101:79–90.

Harding, J. M., R. Mann, M. Southworth & J. A. Wesson. 2011. Management of the Piankatank River, Virginia, in support of oyster (*Crassostrea virginica*, Gmelin 1791) fishery repletion. *J. Shellfish Res.* 29:867–888.

Harding, J. M., M. J. Southworth, R. Mann & J. A. Wesson. 2012. Comparison of *Crassostrea virginica* Gmelin (eastern oyster) recruitment on constructed reefs and adjacent natural oyster bars over decadal time scales. *Northeast. Nat.* 19:627–646.

Harzhauser, M., A. Djuricic, O. Mandie, T. A. Neubauer, M. Zuschin & N. Pfeifer. 2016. Age structure, carbonate production and shell loss rate in an early miocene reef of the giant oyster *Crassostrea gryphoides*. *Biogeosciences* 13:1223–1235.

Hu, X. & D. J. Burdige. 2008. Shallow marine carbonate dissolution and early diagenesis - implications from an incubation study. *J. Mar. Res.* 66:489–527.

Ishikawa, M. & V. S. Kennedy. 2014. Management of the oyster fisheries in Japan's Ariake Sea and Maryland's Chesapeake Bay: a comparison. *Mar. Fish. Rev.* 76:39–49.

Ivanina, A. V., G. H. Dickinson, O. B. Matoo, R. Bagwe, A. Dickinson, E. Beniash & I. M. Sokolova. 2013. Interactive effects of elevated temperature and CO_2 levels on energy metabolism and biomineralization of marine bivalves *Crassostrea virginica* and *Mercenaria mercenaria*. *Comp. Biochem. Physiol. Mol. Integr. Physiol.* 166:101–111.

Kaplan, D. A., M. Olabarrieta, P. Frederick & A. Valle-Levinson. 2016. Freshwater detention by oyster reefs: quantifying a keystone ecosystem service. *PLoS One* 11:e0167694.

Kennedy, V. S., D. L. Breitburg, M. C. Christman, M. W. Luckenbach, K. Paynter, J. Kramer, K. G. Sellner, J. Dew-Baxter, C. Keller & R. Mann. 2011. Lessons learned from efforts to restore oyster populations in Maryland and Virginia, 1990 to 2007. *J. Shellfish Res.* 30:719–731.

Kennish, M. J. & R. A. Lutz. 1999. Calcium carbonate dissolution rates in deep-sea bivalve shells on the east Pacific rise at 21°N: results of an 8-year *in-situ* experiment. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 154:293–299.

Kidwell, S. M. 1986. Taphonomic feedback in miocene assemblages: testing the role of dead hardparts in benthic communities. *Palaios* 1:239–255.

Kidwell, S. M. 2001. Preservation of species abundance in marine death assemblages. *Science* 294:1091–1094.

Kidwell, S. M. 2008. Ecological fidelity of open marine molluscan death assemblages: effects of post-mortem transportation, shelf health, and taphonomic inertia. *Lethaia* 41:199–217.

Kingsley-Smith, P. R., R. E. Joyce, S. A. Arnot, W. A. Roumillat, C. J. McDonough & M. J. M. Reichert. 2012. Habitat use of intertidal eastern oyster (*Crassostrea virginica*) reefs by nekton in South Carolina estuaries. *J. Shellfish Res.* 31:1009–1021.

Kjelland, M. E., C. D. Piercy, T. Lackey & T. M. Swannack. 2015. An integrated modeling approach for elucidating the effects of different management strategies on Chesapeake Bay oyster metapopulation dynamics. *Ecol. Modell.* 308:45–62.

Klinck, J. M., E. N. Powell, J. N. Kraeuter, S. E. Ford & K. A. Ashton-Alcox. 2001. A fisheries model for managing the oyster fishery during times of disease. *J. Shellfish Res.* 20:977–989.

Klompmaker, A. A., R. W. Portell & M. G. Frick. 2017. Comparative experimental taphonomy of eight marine arthropods indicates distance differences in preservation potential. *Palaeontology* 60:773–794.

Kosnik, M. A., Q. Hua, D. S. Kaufman & A. W. Raphael. 2009. Taphonomic bias and time-averaging in tropical molluscan death assemblages: differential shell half-lives in Great Barrier Reef sediment. *Paleobiology* 35:565–586.

Kraeuter, J. N., S. Ford & M. Cummings. 2007. Oyster growth analysis: a comparison of methods. *J. Shellfish Res.* 26:479–491.

Krause, R. A., Jr., K. Parsons-Hubbard & S. E. Walker. 2011. Experimental taphonomy of a decapod crustacean: long-term data and their implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 312:350–362.

Kuykendall, K. M., P. Moreno, E. N. Powell, T. M. Soniat, S. Colley, R. Mann & D. M. Munroe. 2015. The exposed surface area to volume ratio: is shell more efficient than limestone in promoting oyster recruitment? *J. Shellfish Res.* 34:217–225.

La Peyre, M., J. Furlong, L. A. Brown, B. P. Piazza & K. Brown. 2014. Oyster reef restoration in the northern Gulf of Mexico: extent, methods and outcomes. *Ocean Coast. Manage.* 89:20–28.

Lawrence, D. 1968. Taphonomy and information losses in fossil communities. *Geol. Soc. Am. Bull.* 79:1315–1330.

Lebrato, M., D. Iglesias-Rodriguez, R. A. Feely, D. Greeley, D. O. B. Jones, N. Suarez-Bosche, R. S. Lampitt, J. E. Cortes, D. R. H. Green & B. Alker. 2010. Global contribution of echinoderms to the marine carbon cycle: $CaCO_3$ budget and benthic compartments. *Ecol. Monogr.* 80:441–467.

Lee, S.-W., Y.-N. Jang & J.-C. Kim. 2011. Characteristics of the aragonitic layer in adult oyster shells, *Crassostrea gigas*: structural study of myostracum including the adductor muscle scar. *Evid. Based Complement. Alternat. Med.* 2011:10.

MacDonald, J., A. Freer & M. Cusack. 2010. Attachment of oysters to natural substrata by biologically induced marine carbonate cement. *Mar. Biol.* 157:2087–2095.

Maghan, B. W. 1967. The Mississippi oyster industry. *U.S. Fish Wildl. Serv. Fishery Leaflet* 607, 12 pp.

Mann, R., J. M. Harding & M. J. Southworth. 2009b. Reconstructing pre-colonial oyster demographics in the Chesapeake Bay, USA. *Estuar. Coast. Shelf Sci.* 85:217–222.

Mann, R. & E. N. Powell. 2008. Why oyster restoration goals in the Chesapeake Bay are not and probably cannot be achieved. *J. Shellfish Res.* 26:905–917.

Mann, R., M. Southworth, J. M. Harding & J. Wesson. 2004. A comparison of dredge and patent tongs for estimation of oyster populations. *J. Shellfish Res.* 23:387–390.

Mann, R., M. Southworth, J. M. Harding & J. A. Wesson. 2009a. Population studies of the native eastern oyster, *Crassostrea virginica*, (Gmelin, 1791) in the James River, Virginia, USA. *J. Shellfish Res.* 28:193–220.

Margolis, S. V. & R. E. Carver. 1974. Microstructure of chalky deposits found in shells of the oyster *Crassostrea virginica*. *Nautilus* 88:62–65.

MDMR. 2013. Oystermen's guide to Mississippi Gulf coast oyster reefs. Biloxi, MS: Mississippi Department of Marine Resources. 119 pp.

Moore, J. L., B. J. Puckett & S. J. Schreiber. 2018. Restoration of eastern oyster populations with positive density dependence. *Ecol. Appl.* 28:897–909.

Morse, J. W., R. S. Arvidson & A. Lüttge. 2007. Calcium carbonate formation and dissolution. *Chem. Rev.* 107:342–381.

Ogle, J. 1979. A study of four oyster reefs in Mississippi. *Gulf Res. Rep.* 6:261–265.

Parsons-Hubbard, K. M., W. R. Callender, E. N. Powell, E. Carlton, S. E. Walker, A. L. Raymond & G. M. Staff. 1999. Rates of burial and disturbance of experimentally-deployed molluscs: implications for preservation potential. *Palaios* 14:337–351.

Paynter, K. T., V. Politano, H. A. Lane, S. M. Allen & D. Meritt. 2010. Growth rates and prevalence of *Perkinsus marinus* in restored oyster populations in Maryland. *J. Shellfish Res.* 29:309–317.

Peterson, C. H., J. H. Grabowski & S. P. Powers. 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Mar. Ecol. Prog. Ser.* 264:249–264.

Powell, E. N. 1992. A model for death assemblage formation. Can sediment shelliness be explained? *J. Mar. Res.* 50:229–265.

Powell, E. N. & K. A. Ashton-Alcox. 2004. A comparison between a suction dredge and a traditional oyster dredge in the transplantation of oysters in Delaware Bay. *J. Shellfish Res.* 23:803–823.

Powell, E. N. & K. A. Ashton-Alcox. 2013. Is overwinter mortality commonplace in Delaware Bay oyster populations? The ambiguity of dredge efficiency. *J. Shellfish Res.* 32:639–645.

Powell, E. N., K. A. Ashton-Alcox, S. E. Banta & A. J. Bonner. 2001. Impact of repeated dredging on a Delaware Bay oyster reef. *J. Shellfish Res.* 20:961–975.

Powell, E. N., K. A. Ashton-Alcox, J. A. Dobarro, M. Cummings & S. E. Banta. 2002. The inherent efficiency of oyster dredges in survey mode. *J. Shellfish Res.* 21:691–695.

Powell, E. N., K. A. Ashton-Alcox & J. N. Kraeuter. 2007. Reevaluation of eastern oyster dredge efficiency in survey mode: application in stock assessment. *N. Am. J. Fish. Manage.* 27:492–511.

Powell, E. N., W. R. Callender, G. M. Staff, K. M. Parsons-Hubbard, C. E. Brett, S. E. Walker, A. Raymond & K. A. Ashton-Alcox. 2008. Molluscan shell condition after eight years on the sea floor—taphonomy in the Gulf of Mexico and Bahamas. *J. Shellfish Res.* 27:191–225.

Powell, E. N. & J. Davies. 1990. When is an 'old' shell really old? *J. Geol.* 98:823–844.

Powell, E. N., E. E. Hofmann & J. M. Klinck. 2018. Oysters, sustainability, management models, and the world of reference points. *J. Shellfish Res.* 37:833–849.

Powell, E. N., X. P. Hu, W. J. Cai, K. A. Ashton-Alcox, K. M. Parsons-Hubbard & S. E. Walker. 2012b. Geochemical controls on carbonate shell taphonomy in northern Gulf of Mexico continental shelf and slope sediments. *Palaios* 27:571–584.

Powell, E. N. & J. M. Klinck. 2007. Is oyster shell a sustainable estuarine resource? *J. Shellfish Res.* 26:181–194.

Powell, E. N., J. M. Klinck, K. A. Ashton-Alcox, E. E. Hofmann & J. Morson. 2012a. The rise and fall of *Crassostrea virginica* oyster reefs: the role of disease and fishing in their demise and a vignette on their management. *J. Mar. Res.* 70:505–558.

Powell, E. N., J. N. Kraeuter & K. A. Ashton-Alcox. 2006. How long does oyster shell last on an oyster reef? *Estuar. Coast. Shelf Sci.* 69:531–542.

Powell, E. N., A. Logan, R. J. Stanton, D. J. Davies & P. E. Hare. 1989. Estimating time-since-death from the free amino acid content of the mollusc shell: a measure of time averaging in modern death assemblages? Description of the technique. *Palaios* 4:16–31.

Powell, E. N., R. Mann, K. A. Ashton-Alcox, K. M. Kuykendall & M. C. Long. 2017. Can we estimate molluscan abundance and biomass on the continental shelf? *Estuar. Coast. Shelf Sci.* 198:213–224.

Powell, E. N., G. M. Staff, W. R. Callender, K. A. Ashton-Alcox, C. E. Brett, K. M. Parsons-Hubbard, S. E. Walker & A. Raymond. 2011. Taphonomic degradation of molluscan remains during thirteen years on the continental shelf and slope of the northwestern Gulf of Mexico. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 312:209–232.

Powell, E. N., M. E. White, E. A. Wilson & S. M. Ray. 1987. Small-scale spatial distribution of oysters (*Crassostrea virginica*) on oyster reefs. *Bull. Mar. Sci.* 41:835–855.

Price, T. J., G. W. Thayer, M. W. LaCroix & G. P. Montgomery. 1976. The organic content of shells and soft tissues of selected estuarine gastropods and pelecypods. *Proc. Natl. Shellfish. Assoc.* 65:26–31.

Ries, J. B., M. N. Ghazaleh, B. Connolly, I. Westfield & K. Castillo. 2016. Impacts of seawater saturation state (Ω A = 0.4–4.6) and temperature (10, 25 °C) on the dissolution kinetics of whole-shell biogenic carbonates. *Geochim. Cosmochim. Acta* 192:318–337.

Smith, S. V. 1971. Budget of calcium carbonate, southern California continental borderland. *J. Sediment. Petrol.* 41:798–808.

Soniat, T. M. & G. M. Burton. 2005. A comparison of the effectiveness of sandstone and limestone as cultch for oysters, *Crassostrea virginica*. *J. Shellfish Res.* 24:483–485.

Soniat, T. M., N. Cooper & E. N. Powell. 2019. Prospects for the sustainable management of public oyster resources. *J. Shellfish Res.* 38:337–349.

Soniat, T. M., N. Cooper, E. N. Powell, J. M. Klinck, M. Abdelguerfi, S. Tu, R. Mann & P. D. Banks. 2014. Estimating sustainable harvests of eastern oysters, *Crassostrea virginica*. *J. Shellfish Res.* 33:381–394.

Soniat, T. M., J. M. Klinck, E. N. Powell, N. Cooper, M. Abdelguerfi, E. E. Hofmann, J. Dahal, S. Tu, J. Finigan, B. S. Eberline, J. F. La Peyre, M. K. La Peyre & F. Qaddoura. 2012. A shell-neutral modeling approach yields sustainable oyster harvest estimates: a retrospective analysis of the Louisiana state primary seed grounds. *J. Shellfish Res.* 31:1103–1112.

Southworth, M., J. M. Harding, J. A. Wesson & R. Mann. 2010. Oyster (*Crassostrea virginica*, Gmelin 1791) population dynamics on public reefs in the Great Wicomico River, Virginia, USA. *J. Shellfish Res.* 29:271–290.

Staff, G., E. N. Powell, R. J. Stanton, Jr. & H. Cummins. 1985. Biomass: is it a useful tool in paleocommunity reconstruction? *Lethaia* 18:209–232.

Stunz, G. W., T. J. Minello & L. P. Rozas. 2010. Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. *Mar. Ecol. Prog. Ser.* 406:147–159.

Subhas, A. V., N. E. Rollins, W. M. Berelson, S. Dong, J. Erez & J. F. Adkins. 2015. A novel determination of calcite dissolution kinetics in seawater. *Geochim. Cosmochim. Acta* 170:51–68.

Tapanila, L., A. Ferguson & E. M. Roberts. 2015. Paradox of drilled devil's toenails: taphonomic mixing obscures Cretaceous drilling predation in Utah oysters. *Palaios* 30:294–303.

Taylor, J. D. & M. Layman. 1972. The mechanical properties of bivalve (Mollusca) shell structures. *Palaeontology* 15:73–87.

Tomašových, A. 2004. Postmortem durability and population dynamics affecting the fidelity of brachiopod size-frequency distributions. *Palaios* 19:477–496.

Vermeij, G. J. 2013. The oyster enigma variations: a hypothesis of microbial calcification. *Paleobiology* 40:1–13.

Waldbusser, G. G., E. N. Powell & R. Mann. 2013. Ecosystem effects of shell aggregations and cycling in coastal waters: an example of Chesapeake Bay oyster reefs. *Ecology* 94:895–903.

Waldbusser, G. G. & J. E. Salisbury. 2014. Ocean acidification in the coastal zone from an organism's perspective: multiple system parameters, frequency domains, and habitats. *Annu. Rev. Mar. Sci.* 6:223–247.

Waldbusser, G. G., R. A. Steenson & M. A. Green. 2011. Oyster shell dissolution rates in estuarine waters: effects of pH and shell legacy. *J. Shellfish Res.* 30:659–669.

Warburton, F. E. 1958. Control of the boring sponge on oyster beds. *Prog. Rep. Atl. Coast. Stns.* 69:7–11.

Weber, E. D., J. H. Vølstad, M. C. Christman, D. Lewis & J. R. Dew-Baxter. 2013. Application of a demographic model for evaluating proposed oyster-restoration actions in Chesapeake Bay. *Hum. Ecol. Risk Assess.* 19:1187–1203.

Wilberg, M. J., J. R. Wiedenmann & J. R. Robinson. 2013. Sustainable exploitation and management of autogenic ecosystem engineers: application to oysters in Chesapeake Bay. *Ecol. Appl.* 23:766–776.

Young, H. R. & C. S. Nelson. 1985. Biodegradation of temperate-water skeletal carbonates by boring sponges on the Scott Shelf, British Columbia, Canada. *Mar. Geol.* 65:33–45.

zu Ermgassen, P. S. E., M. D. Spalding, B. Blake, L. D. Coen, B. Dumbauld, S. Geiger, J. H. Grabowski, R. Grizzle, M. Luckenbach, K. McGraw, W. Rodney, L. Ruesink, S. P. Powers & R. Brumbaugh. 2012. Historical ecology and real numbers: past and present extent and biomass of an imperiled estuarine habitat. *Proc. R. Soc. Lond. B Biol. Sci.* 279:3393–3400.

Zuschin, M., M. Stachowitsch & R. J. Stanton. 2003. Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth Sci. Rev.* 63:33–82.