



# Lethal and sublethal effects of sediment burial on the eastern oyster *Crassostrea virginica*

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**ABSTRACT:** Eastern oysters *Crassostrea virginica* are dominant ecosystem engineers that construct complex reefs in estuarine systems. Reef persistence relies on reef growth, which must outpace reef degradation and sediment deposition. The quantitative impact of burial on oyster survival and sublethal effects of sediment deposition are undefined. In this mesocosm study, we quantified effects of partial and complete burial (0, 50, 70, 90, and 110% of oyster shell height) on survival, biodeposition, condition index and growth of oysters (shell height = 25–75 mm). Survival only declined significantly when 90% or more of an oyster was buried; the critical burial depth inducing 50% mortality was 108%. This finding will allow scaling of mortality rates of oysters as a function of sediment load and oyster size. Biodeposition and condition index were negatively related to burial depth, whereas shell growth increased with burial depth. Decreases in biodeposition and condition index were likely related to disruption of feeding by burial and reallocation of energy resources to shell growth. The increase in shell growth was analogous to vertical migration of infaunal species—buried oysters increased vertical shell growth to breach the sediment surface to feed and respire, at the expense of tissue growth. While oysters are tolerant of partial burial in terms of survival, burial adversely affects metabolic processes that influence demographic rates and reef persistence. Future management efforts should consider the effects of partial burial, which often occur more frequently than catastrophic burial events causing mass mortality.

**KEY WORDS:** Sediment · Burial · Mortality · Biodeposition · Oysters · Restoration

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## INTRODUCTION

With more than one-third of the world's population living within 100 km of the coastline (Cohen et al. 1997), the potential for human impacts on coastal and estuarine environments is profound. One such impact is the dramatic increase in terrestrial sediment flux to estuaries as a result of deforestation, land use change, and agriculture (Syvitski et al. 2005). Generally, estuaries act as sediment traps, steadily infilling until an erosional event, such as a strong storm, removes sediment from the system (Dellapenna et al. 1998). Substantial land clearance by European settlers of the US mid-Atlantic region in the late 18th century resulted in a 10-fold increase in sediment inputs to coastal habitats (Meade 1982). Additionally, sediments resulting from this initial

land clearance are stored in watershed reservoirs, which are expected to continue to augment sediment inputs for several centuries (Meade 1982). Predicted changes in the frequency and intensity of storm activity, precipitation and streamflow associated with climate change are likely to further increase sediment inputs (Pyke et al. 2008, Najjar et al. 2010) and mobilize watershed sediment stores (Meade 1982). As such, estuaries will continue to experience a constant influx of sediment from exogenous sources.

Sediment inputs influence the structure and function of estuarine habitats through modification of sediment characteristics, nutrient availability, and water clarity. Sediment grain size is an important factor structuring benthic communities (Gray 1981); sediment inputs that significantly alter grain size or bury epifaunal or infaunal organisms can diminish

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benthic diversity and productivity (Maurer et al. 1981). Suspended sediments reduce light availability for estuarine autotrophs; sediment cores from Chesapeake Bay indicate a reduction in microphytobenthos due to reduced water clarity and a shift to pelagic phytoplankton species due to nutrient inputs from run-off after watershed deforestation (Cooper & Brush 1993). Sediment and nutrient inputs have also been implicated in the widespread reduction in seagrass cover (Orth et al. 2006), with serious consequences for estuarine biodiversity (Waycott et al. 2009).

Like seagrasses, biogenic reefs constructed by the eastern oyster, *Crassostrea virginica*, are important features structuring the estuarine landscape. Oyster populations and reefs provide a suite of ecosystem services (Coen et al. 2007, Grabowski & Peterson 2007), such as habitat for benthic macrofauna (Zimmerman et al. 1989), enhanced benthic-pelagic coupling and nutrient cycling (Lenihan 1999, Kellogg et al. 2013), and shoreline stabilization (Meyer et al. 1997, Piazza et al. 2005). Unfortunately, oyster population biomass and associated reef habitat along the Gulf of Mexico and Atlantic coasts in the United States have declined by 88 and 64 %, respectively (Zu Ermgassen et al. 2012). Declines in reef quality have been attributed to overharvesting, habitat degradation, and disease (Rothschild et al. 1994). Moreover, the removal of shell material and disassociation of the reef structure by harvesting reduces reef elevation, rendering reefs more susceptible to siltation and eventual burial (Rothschild et al. 1994, Smith et al. 2001).

Reef burial can be caused by episodic events such as storms (Livingston et al. 1999), run-off (Twichell et al. 2010), or dredging (Wilber & Clarke 2001) whose associated deposition can rival or exceed annual rates (Norris 1953, Miller et al. 2002, Suedel et al. 2014). Winds, waves, and storm surge causes the erosion and mass transport of sediments (Livingston et al. 1999), the deposition of which can kill oysters and bury entire reefs (Norris 1953, Miller et al. 2002, Twichell et al. 2010). Run-off events associated with changes in freshwater inputs to the watershed by precipitation, seasonal inputs, or controlled releases from man-made reservoirs can deposit up to 31 cm of sediment in a single event (Kniskern & Kuehl 2003). These events can also bury reefs, particularly those adjacent to river mouths due to their proximity to sediment plumes (Twichell et al. 2010). Additionally, freshwater pulses can cause oyster mortality and exacerbate burial effects. Each year, approximately 400 million m<sup>3</sup> of sediment are dredged throughout

the United States to maintain channels (Jones & Lee 1981). Dredged sediments produce a plume that increases suspended sediment concentrations and affects areas up to 500 m from the dredge site (Wilber & Clarke 2001, Suedel et al. 2014). Suspended sediments can abrade gill tissues, inflicting metabolic stress (Suedel et al. 2014), and associated deposition may increase oyster mortality by 40 % (Rose 1973).

Despite the presumed importance of sediment deposition on oyster reef persistence (Jordan-Cooley et al. 2011), few studies have addressed burial effects quantitatively and results of those studies have been variable. At the reef scale, sediment deposition has been cited as the main cause of intertidal and subtidal reef failure (Bahr & Lanier 1981, Taylor & Bushek 2008, Powers et al. 2009). In contrast, Fodrie et al. (2014) found no correlation between sedimentation and various oyster metrics at a small sub-reef scale (0.25 m<sup>2</sup> patches). To elucidate the effects of burial, we experimentally examined the lethal and sublethal effects of sediment deposition on oysters. Specifically, in mesocosm experiments, we (1) quantified survival in various burial depth treatments, (2) determined a critical burial depth at which 50 % of oysters experience mortality (LD<sub>50</sub>), and (3) measured sublethal responses to partial burial by quantifying biodeposition, growth, and condition index. Biodeposition and growth are the key metabolic processes contributing to reef accretion (DeAlteris 1988), which is critical for sustaining reef habitat. Condition index, a ratio of somatic tissue weight to shell cavity volume, is an indicator of oyster health, identifying whether oysters are negatively impacted by burial even if they do not experience mortality. The results of this study can be incorporated into mathematical models (Jordan-Cooley et al. 2011, Wilberg et al. 2013) to determine reef-scale impacts to inform management actions for imperiled eastern oyster populations throughout their geographic range.

## MATERIAL AND METHODS

### Mesocosm Expt 1

We measured survival, growth, condition index, and biodeposition of 278 hatchery-reared triploid oysters over a 28-day period in July 2013. Episodic wind events and spring tidal currents control sediment resuspension and transport in shallow estuarine habitats, indicating that partial or complete burial conditions dominate on time scales of days to weeks (Sanford et al. 1991, Kniskern & Kuehl 2003). Conse-

quently, we limited our experiments to the most relevant time frame for deposition in shallow areas, ca. 1 mo, which would encompass spring-neap cycles and episodic events. Triploid oysters were used to minimize individual variation due to reproductive effort and to provide a wide range of sizes of available oysters, given the time of year. Using hatchery oysters from a single source also minimized variation due to differences in acclimation and handling stress, as all oysters were reared in the same area and under the same cultivation methods.

Oysters of 25–75 mm shell height (SH) were obtained from a local oyster grower on the York River, Virginia, and transported to the Virginia Institute of Marine Science in Gloucester Point, Virginia. Shell height (mm) and wet weight (g) were measured for each oyster, and oysters were randomly assigned to one of the following burial treatments: 0, 50, 70, 90, and 110%. We hypothesized that burial depth relative to the size of the oyster was important; therefore, treatments represented the percentage of an individual oyster's shell height that was buried by sediment (Fig. 1). Oysters in the 0% burial treatment (control) were placed on top of the sediment.

To ensure proper burial depth and to prevent subsidence of the oyster during the experiment, an individual experimental container (473 ml) with an elevated bottom was prepared for each oyster. Portland cement poured into each container was used to elevate the oyster off the bottom of the experimental container such that the appropriate percentage of the oyster's height given the assigned treatment would be exposed when the container was filled flush with sediment. Each oyster was placed in the prepared container facing upright with the umbo of the oyster resting on the cement bottom (Fig. 1). The containers were filled to the rim with sand (mean  $\pm$  SE;  $96.6 \pm 0.2\%$  sand) obtained approximately 5 m offshore of Gloucester Point, Virginia. This sediment grain size typifies sediments in shallow estuarine areas throughout the eastern oysters' geographic range, including the Gulf of Mexico (Lisle & Comer 2011) and other mid-Atlantic estuaries (Kiddon & Buffum 2000). Prior to use, sand was sieved with a 500  $\mu\text{m}$  sieve to remove debris and defaunated by air-drying.

Experimental containers were distributed evenly into 6 large outdoor mesocosm tanks ( $2.43 \times 1.11 \times 0.91$  m) at the Virginia Institute of Marine Science. Tanks were first divided into 50 even quadrants and containers with oysters were randomly distributed into the quadrants, excluding those directly below the tank inflow and near the tank drain pipe. This distribution ensured even spacing of experimental

units throughout the tanks. A downspout was added to the inflow to direct the flow of water towards the bottom of the tank to minimize resuspension of biodeposits collected during the experiment. Tanks were supplied with a continuous flow of unfiltered York River water at a rate of approximately  $5.33 \text{ l min}^{-1}$ , resulting in full replacement at least 3 times daily. Aquarium bubblers were added to each tank to ensure adequate oxygenation.

Environmental conditions in the tanks were monitored using data loggers (Tidbit v2 Water Temperature Data Logger, Onset) and a hand-held data sonde (Yellow Springs Instruments). Temperature data to the nearest  $0.01^\circ\text{C}$  was collected every 30 min for the duration of the experiment by data loggers. Additional measurements of temperature, salinity, and dissolved oxygen (DO) were periodically taken from the water column at the approximate height of experimental containers using the data sonde to validate the readings from data loggers and to monitor additional environmental variables expected to influence oyster metabolism.

Random samples of oysters in each burial treatment were removed from the tanks at weekly intervals, for a total of 4 sampling events over the 28 d period. This resulted in 14 replicates per withdrawal-

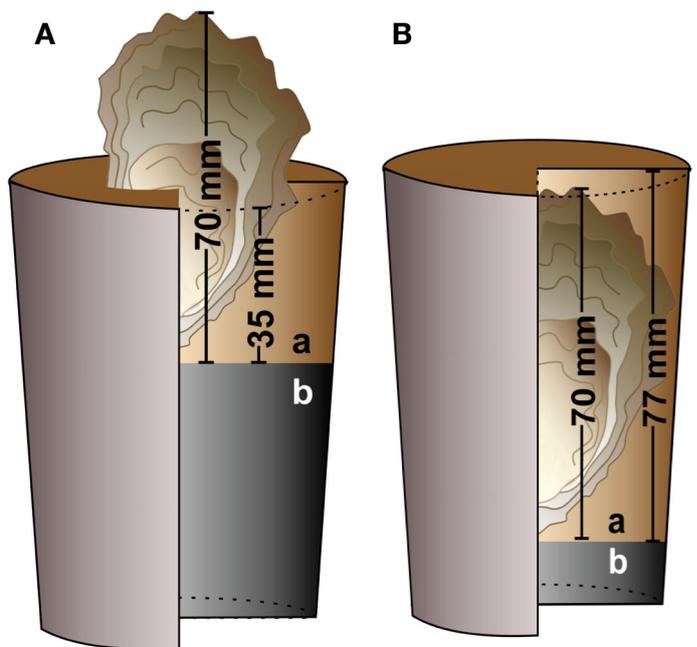


Fig. 1. Set-up of experimental containers. Panel A depicts an oyster in the 50% burial treatment. Sediment is labeled 'a' and the elevated bottom of Portland cement is labeled 'b.' Panel B depicts an oyster in the 110% burial treatment; sediment and elevated bottom are labeled as in Panel A

treatment combination, with the exception of the 50%-Week 1 and 90%-Week 4 treatments. In these 2 treatment-week combinations, 1 oyster in each was found to be dead prior to the start of the experiment (valves filled with mud), resulting in 13 replicates; the 2 datapoints from these oysters were excluded from all analyses. The subsampled oysters were assessed for survival, growth, and condition index. Biodeposit collection trays were placed on those oysters selected for sampling 6 d prior to the sampling event. Biodeposits were then collected and processed along with the oysters each week. After removing the oysters, the experimental containers were filled with additional sediment and returned to the mesocosms to avoid changes in flow within the tanks.

### Lethal effects

Oysters were removed from their containers, scrubbed, and visually assessed for survival as follows: live oysters were those whose valves were either tightly closed or closed after handling. Gaping or empty oysters were considered dead. Shell height (mm) and wet weight (g) were measured for all oysters and used to determine growth rates. Live oysters were retained for biodeposition and condition index analyses.

### Sublethal effects

Biodeposits were collected in aluminum trays placed on top of each experimental container. A small slit was cut in the bottom of each collection tray to allow the oyster to protrude through the tray and gape sufficiently, with the exception of collection trays for the 0% and 110% treatments for which the tray was left intact. Oysters in the 0% burial treatment were placed on top of the intact collection tray, which was situated on the sediment surface. Oysters in the 110% burial treatment did not protrude from the sediment, and the collection tray was placed on top of the oyster on the sediment surface.

After 6 d, collection trays were capped and removed and biodeposits rinsed into pre-weighed dishes. Any biodeposits remaining on the sediment surface in partial burial treatments after the removal of the collection tray were collected by pipette. Biodeposits were easily distinguished from underlying sediments due to their size and pelletized nature. Biodeposits were dried to constant weight at 60°C

and weighed to the nearest 0.001 g ( $\pm 0.0001$  g). Biodeposition rate was calculated as the dry weight (DW) of biodeposits divided by the number of days of biodeposit collection (6 d), expressed as g DW d<sup>-1</sup>.

Condition index was determined for all live oysters following each sampling event. Oyster condition index was assessed using the index of Abbe & Albright (2003), the ratio of dry tissue weight (g) to shell cavity volume, which is approximated by subtracting the wet weight of the shells immediately after removing oyster tissue from the total wet weight. This condition index accounts for the partitioning of resources into tissue vs. shell growth. Higher condition indices suggest that growth effort is directed toward tissue growth, whereas lower condition indices suggest the dominance of shell growth over tissue growth or the deterioration of tissue quality (weight) over time.

Prior to the start of the experiment and after withdrawal, each oyster's shell height, width, depth, and total wet mass were recorded. Shell height difference was chosen to represent growth rate, as it was the least variable of all growth responses. The difference in shell height before and after the experiment was divided by the number of days in the trial to determine the growth rate in mm d<sup>-1</sup>. Oysters with calculated growth rates <0 were considered to be 0, since it is likely that the negative change in shell height was due to measurement error rather than loss of shell at the margin.

### Statistical analyses

Oyster survival was analyzed by logistic regression with burial treatment and time as predictor variables and tank as a blocking factor. Combinations of these variables were used to define the *a priori* candidate model set (Table 1). Initial analyses of the effect of oyster size on survival indicated that size was not a significant factor ( $p = 0.56$ ); therefore, oyster size was not included as a factor. Akaike's information criterion corrected for small sample size (AICc) was used to compare candidate models (Anderson 2008). Effect sizes and likelihood ratio tests were used to assess model fit. The 50% mortality level (LD<sub>50</sub>) for burial treatments was determined by solving for the inflection point of the best-fitting logistic model. The 95% confidence interval for LD<sub>50</sub> was determined by bootstrapping ( $n = 1000$ ) with replacement.

Oyster growth, condition index, and biodeposition rate were analyzed using multiple linear regression, with burial treatment and week as predictor variables and tank as a blocking factor. To account for

oyster size, an initial regression of size against each response variable was conducted. If oyster size was significant, then the residuals of that regression were analyzed with the candidate model set (Table 1). If size was not significant, then the original data were used in regressions with the candidate model set. We used AIC to select the best model for each response variable. If AIC values indicated more than one plausible model ( $w > 0.1$ ), effect sizes and model fit ( $r^2$ )

Table 1. AIC model comparison results for oyster response variables in triploid trials (Expt 1). The best model is indicated in **bold**. AIC weights ( $w$ ) indicate the probability of a model representing the best model in the candidate set.  $p$ -values reported for survival models are the result of likelihood ratio tests with the treatment-only model (Model 1) as the null model

Survival				
Model	Parameters	AICc	$w$	$p$ ( $\chi^2$ )
<b>1</b>	<b>Burial</b>	<b>134.4</b>	<b>0.58</b>	–
2	Week	232.9	<0.01	–
3	Burial + Week	136.2	0.24	0.62
4	Burial + Week + Tank	138.1	0.09	0.78
5	Burial $\times$ Week	138.3	0.08	0.87
Biodeposition				
Model	Parameters	AICc	$w$	$r^2$
1	Burial	630.1	<0.01	0.14
2	Week	558.1	<0.01	0.38
<b>3</b>	<b>Burial + Week</b>	<b>503.0</b>	<b>0.52</b>	<b>0.52</b>
4	Burial + Week + Tank	504.3	0.28	0.51
5	Burial $\times$ Week	505.0	0.20	0.51
Condition index				
Model	Parameters	AICc	$w$	$r^2$
1	Burial	1102.5	<0.01	0.01
2	Week	1007.8	0.03	0.34
<b>3</b>	<b>Burial + Week</b>	<b>1003.8</b>	<b>0.24</b>	<b>0.35</b>
4	Burial + Week + Tank	1002.4	0.48	0.36
5	Burial $\times$ Week	1003.8	0.24	0.35
Growth				
Model	Parameters	AICc	$w$	$r^2$
<b>1</b>	<b>Burial</b>	<b>-190.9</b>	<b>0.21</b>	<b>0.11</b>
2	Week	-164.4	0.38	0.01
3	Burial + Week	-191.7	0.33	0.12
4	Burial + Week + Tank	-190.7	0.20	0.12
5	Burial $\times$ Week	-191.3	0.26	0.12
Survival				
Model	Parameters	AICc	$w$	$p$ ( $\chi^2$ )
<b>1</b>	<b>Burial</b>	<b>40.2</b>	<b>0.69</b>	–
2	Size	50.3	<0.01	–
3	Burial + Size	42.5	0.22	0.97
5	Burial $\times$ Size	44.3	0.09	0.72

were examined to determine the most parsimonious model (Anderson 2008). Shapiro-Wilk and Levene's tests and visual inspection of model residuals were used to assess normality and homogeneity of variance assumptions. Biodeposition rate data were log-transformed to meet the assumptions of normality and homogeneity of variance; all other variables satisfied linear regression assumptions without transformation. Differences in environmental variables among tanks were assessed with a 1-way analysis of variance (ANOVA) model. All statistical analyses were conducted using R statistical software, version 3.1.0 (R Core Development Team 2013).

### Mesocosm Expt 2

A second burial trial using wild, diploid oysters collected from the Great Wicomico River, Virginia was conducted to determine if ploidy would affect the burial-survival function. Experimental containers for 56 adult oysters (60–90 mm SH) were prepared as described previously. Oysters were randomly assigned to 0, 25, 50, 70, 90, 100, and 110% burial treatments ( $n = 8$ ) and randomly distributed into 3 outdoor mesocosm tanks used in the triploid trial. After 12 d, all oysters were removed and assessed for survival. Oysters that were tightly closed or closed upon handling were considered live; gaping oysters that did not respond to handling or empty valves were considered dead. Diploid oysters were expected to experience greater mortality and metabolic stress than triploid oysters due to gametogenesis and reproduction; therefore, diploid trials were shorter than triploid trials. The trial duration (12 d) represents the approximate interval of partial burial due to spring-neap tidal cycles in the absence of other episodic events. Diploid survival was analyzed using logistic regression and AIC model selection with burial treatment and oyster size as factors (Table 2). Tank and week were not included as factors because no signif-

Table 2. AIC model comparison results for oyster survival in diploid trials (Expt 2). The best model is indicated in **bold**.  $p$ -values reported are the result of likelihood ratio tests with the treatment-only model (Model 1) as the null model

Model	Parameters	AICc	$w$	$p$ ( $\chi^2$ )
<b>1</b>	<b>Burial</b>	<b>40.2</b>	<b>0.69</b>	–
2	Size	50.3	<0.01	–
3	Burial + Size	42.5	0.22	0.97
5	Burial $\times$ Size	44.3	0.09	0.72

icant tank effects were found in previous trials and all oysters were sampled at the conclusion of the 12 d trial. The diploid burial-survival function was estimated from the best-fitting logistic model, and the point of 50% mortality ( $LD_{50}$ ) was estimated from the inflection point of the function. The 95% confidence interval about the inflection point was determined by bootstrapping with replacement ( $n = 1000$ ).

## RESULTS

### Mesocosm Expt 1

#### Mesocosm conditions

Temperatures ranged 23.2–36.6°C, which is well below the maximum thermal tolerance of eastern oysters (48.5°C; Shumway 1996). The mean temperature observed in our mesocosms (27.2°C; Table 3) is within the 15 yr mean temperature range for Virginia (23–29°C) (Southworth & Mann 2014) and for other mid-Atlantic estuaries (19–31°C) (Kiddon & Buffum 2000). Elevated temperatures (>30°C) were observed for <10% of the experiment's duration, indicating that any effects of thermal stress are likely minimal relative to stress due to burial. The data logger for one tank failed to deploy, and did not collect data for the duration of the experiment; therefore, the temperature data collected by the YSI data sonde was used for comparison. Variation in salinity (17.5–22.4) was also within the tolerance limits of this euryhaline species (Table 3). Dissolved oxygen (DO) levels within experimental tanks remained within normoxic limits throughout the experiment (Table 3), indicating that water column DO levels were sufficient to maintain normal metabolic functions. There were no significant differences between mesocosm tanks in any of the environmental variables (Table 3).

Table 3. Summary of environmental conditions in mesocosms for Expt 1. Values given in parentheses are SE. p-values are reported for 1-way ANOVAs for differences in environmental variables between mesocosm tanks

Variable	Range	Mean (SE)	p-value
Temperature (°C)	23.2–36.6	27.2 (0.1)	0.98
Salinity (ppt)	17.5–22.4	19.9 (0.2)	0.99
Dissolved oxygen (mg l <sup>-1</sup> )	3.2–9.3	4.8 (0.2)	0.62

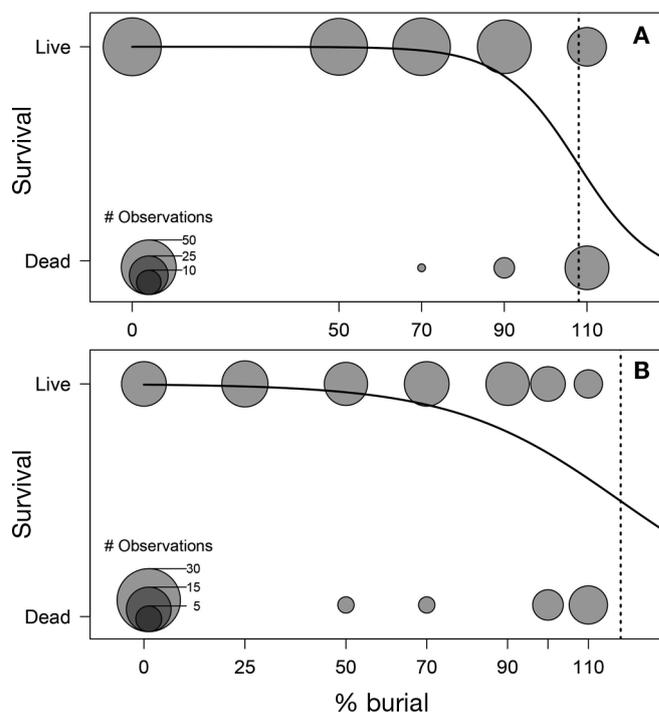


Fig. 2. Oyster survival across % burial treatments for (A) triploid (Expt 1) and (B) diploid (Expt 2) trials. The size of the circle is proportional to the number of observations at each survival status-treatment combination (smallest circle = 1 [triploid] or 2 [diploid] observations). Dashed lines indicate the % burial at which 50% mortality occurred as estimated from the logistic regression. Burial treatment was the only significant factor (triploid:  $p < 0.01$ ; diploid:  $p = 0.02$ ) for survival

#### Lethal effects

The estimated burial-survival function indicated that survival was not significantly impacted by burial up to 70%; the  $LD_{50}$  was 108% burial (Fig. 2a). In total, 40 oysters died over the course of the experiment, all at burial depths of 70% and greater (Fig. 2a). The highest mortality occurred in the first week and in the highest burial treatment. Burial treatment was the only significant factor affecting survival (Table 1), and this model provided a significantly better fit than the null (intercept only) model (Wald test,  $df = 276$ ,  $p < 0.01$ ). The remaining models did not improve the fit significantly over the treatment-only model (Table 1).

#### Sublethal effects

Biodeposition rate (g DW d<sup>-1</sup>) was highest in the 0% burial treatment and decreased monotonically

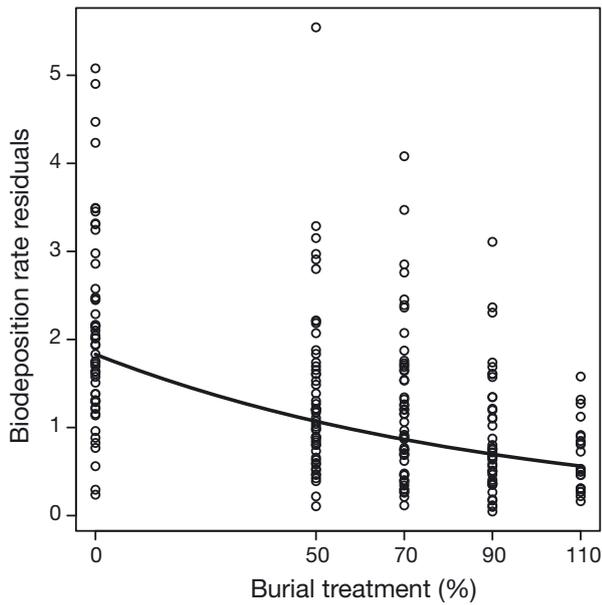


Fig. 3. Biodeposition rate residuals across % burial treatments in triploid trials (Expt 1). Regression shown is the back-transformed log-linear regression of biodeposition-week regression residuals ( $r^2 = 0.22$ ). Both treatment ( $p < 0.01$ ) and week ( $p < 0.01$ ) were significant factors controlling biodeposition. Oyster size ( $p = 0.08$ ) and tank ( $p = 0.40$ ) were not significant

and significantly across partial burial treatments (Fig. 3, Table 4). The lowest deposition rate occurred in the 110% burial treatment (Table 4); however, this value represents passive deposition in the tank rather than biodeposition, as indicated by the absence of fecal pellets. Oysters in the 110% treatment were entirely buried for the duration of the experiment, and the biodeposit collection trays were situated on the sediment surface within the experimental container. Biodeposition rates in all other treatments (Table 4) may have included some passive deposition, but it was likely minimal because most of the sediment was bound in pseudofeces due to active filtration by oysters. Week was also a significant factor controlling biodeposition rates ( $p < 0.01$ ). Mean biodeposition decreased over time in all burial treatments, indicating increasing metabolic stress over time or temporal changes in seston inputs over the duration of the experiment.

Condition index varied additively with burial treatment and week (Table 1). AIC comparisons indicated that the model including tank effects was the best of the candidate set; however, parameter estimates for tank effects were non-significant ( $p = 0.07$ ), so the treatment-week model, being the most parsimonious, was chosen (our Table 1; Anderson 2008). Bur-

Table 4. Summary of sublethal effects of burial treatments on mean biodeposition, condition index and growth in triploid trials (Expt 1). Values given in parentheses are standard error

Burial treatment (%)	Biodeposition (g DW d <sup>-1</sup> )	Condition index	Growth (mm d <sup>-1</sup> )
0	0.27 (0.03)	9.8 (0.3)	0.12 (0.01)
50	0.18 (0.03)	9.9 (0.5)	0.16 (0.02)
70	0.15 (0.02)	9.8 (0.3)	0.22 (0.02)
90	0.11 (0.01)	8.9 (0.4)	0.24 (0.03)
110	0.08 (0.01) <sup>a</sup>	8.9 (0.5)	0.32 (0.05)

<sup>a</sup>Mean deposition reported for 110% burial treatment represents background sedimentation in the tanks rather than oyster biodeposition

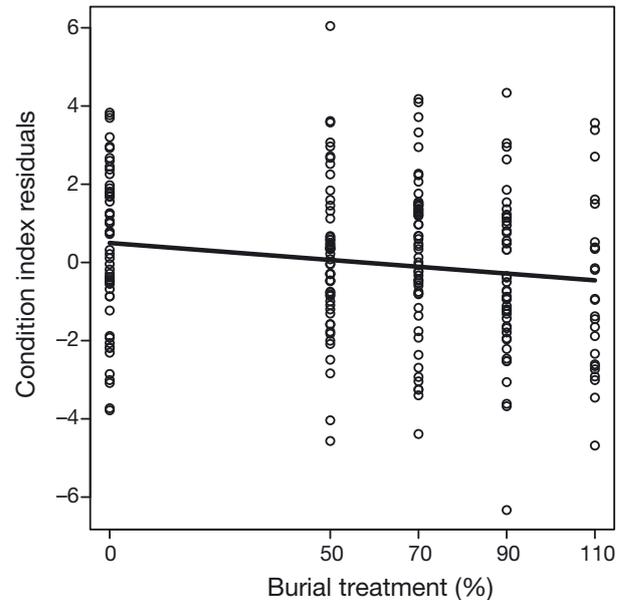


Fig. 4. Oyster condition index across % burial treatments in triploid trials (Expt 1). Model estimates indicated a significant effect of week on oyster condition index ( $p < 0.01$ ); therefore, data shown are the residuals from the condition index-week regression as a function of burial treatment ( $p = 0.01$ ;  $r^2 = 0.35$ ). Oyster size ( $p = 0.15$ ) and tank ( $p = 0.07$ ) were not significant

ial treatment and time had opposing effects on oyster condition index. Condition index generally declined with increasing burial (Fig. 4), but increased with time. The highest condition index was in the 50% burial treatment (Table 4). The 0, 50, and 70% burial treatments tended to have similar condition indices, whereas the 90 and 110% treatments tended to have lower condition indices (Table 4). Among all burial treatments, the highest condition index was in the 21 d sampling interval (mean  $\pm$  SE:  $11.5 \pm 0.2$ ), followed by the 28 d interval ( $11.0 \pm 0.3$ ).

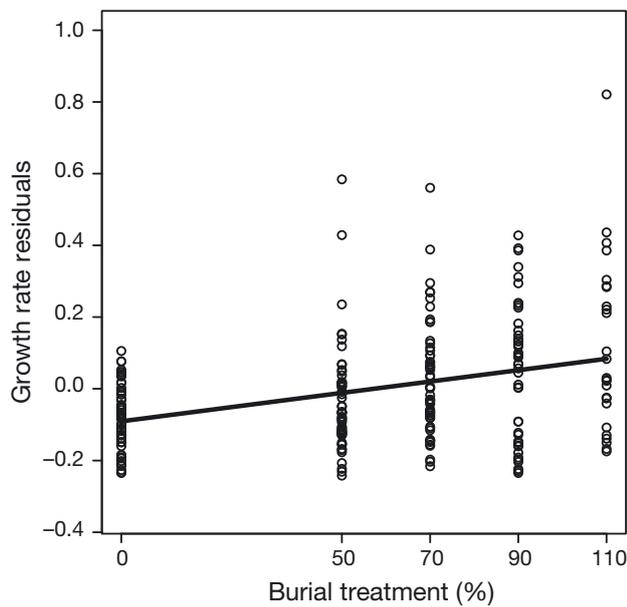


Fig. 5. Oyster growth-rate residuals as a function of % burial treatment in triploid trials (Expt 1). Initial regression indicated a significant effect of oyster size on growth rate ( $p < 0.01$ ); therefore, data shown are the residuals from the size-growth rate regression of growth rate as a function of burial treatment ( $p < 0.01$ ;  $r^2 = 0.11$ ). Tank and week effects were not significant ( $p = 0.32$  and  $p = 0.10$ , respectively)

Oyster size had a significant effect on growth rates ( $r^2 = 0.05$ ;  $p < 0.01$ ). To account for oyster size, we analyzed the residuals of the oyster size-growth rate linear regression with the candidate model set (Fig. 5, Table 1). Burial treatment was the only significant factor controlling growth rates (Table 1), which increased with burial depth (Fig. 5). The highest growth rate was in the 110% burial treatment, which was nearly 3 times the mean growth rate of the 0% burial treatment (Table 4). Mean growth rates in 70 and 90% burial treatments were double the growth rate of the 0% treatment (Table 4).

### Mesocosm Expt 2

After 12 d, 8 of 56 oysters in the diploid trial died, which occurred in the 50, 70, 100 and 110% burial treatments. The highest mortality was in the 110% burial treatment ( $n = 5$ ), and was equivalent in the 50, 70, and 100% treatments in which a single oyster died. No mortality was observed in 0, 25, or 90% treatments. As in the triploid trials, burial treatment was the only significant factor affecting survival (Table 2,  $p = 0.023$ ); oyster size and treatment-size in-

teractions were not significant ( $p = 0.44$  and  $p = 0.41$ , respectively). The treatment only model provided a significantly better fit than the null model (Wald test;  $df = 2$ ;  $p = 0.001$ ) and the additive and interaction models were not significantly different from the treatment model (Fig. 2b, Table 2). The diploid burial-survival function (Fig. 2b) had an estimated inflection point of 118% burial (95% CI: 96–154%), which is higher than the  $LD_{50}$  for triploids of 108%.

## DISCUSSION

The key findings of our study were that (1) oysters buried in sediment did not exhibit significant mortality or sublethal effects until at least 70% of the shell was buried, (2) the survival response differed little between diploid and triploid oysters or by oyster size, (3) biodeposition and condition index were inversely related to burial depth, and (4) shell growth increased with burial depth.

### Lethal effects

With the exception of 1 oyster in the 70% burial treatment, all mortality occurred in the 90 and 110% burial treatments over the 28 d experiment. The maximum mortality was 62% during the first week in the 110% treatment group, although oyster survival did not vary significantly with time. This mortality was much lower than those observed previously (Lund 1957a, Dunnington 1968), in which 100% mortality of completely buried adult oysters occurred within 7 d. However, the burial depths in previous experiments were higher, up to 76 mm of sediment (Dunnington 1968). In experiments with comparable burial depths, lethal burial depths for adult oysters were 10–20 mm below the sediment surface (Kranz 1974, Essink 1999), though these values were not calculated relative to shell height. The maximum burial depth in the present study was 7.4 mm for a 73.5 mm oyster. Lund (1957a) suggested that shallowly buried oysters (<12.7 mm) may be able to clear sediment from their bill by repeatedly opening and closing their valves, a behavioral adaptation to burial. Exposed valves were not observed in any of the 110% burial treatments; however, small depressions in the sediment surface were evident, which may indicate the movement of buried oysters in an attempt to remove sediment (Lund 1957a, Hinchey et al. 2006).

Diploid and triploid oysters responded similarly to burial, with the highest mortality observed in the

complete (110%) burial treatments (Fig. 2). Diploid oysters exhibited mortality at lower partial burial (50%) than triploids (70%), but mortality in the 50% diploid treatment was limited to a single oyster. The LD<sub>50</sub> for diploids was 118% burial, which is higher than the 108% LD<sub>50</sub> for triploids (Fig. 2); however, these estimates were not significantly different from one other, suggesting that both triploids and diploids are tolerant to partial burial in terms of survival. The higher LD<sub>50</sub> for diploids may have resulted from a shorter experimental duration or the larger size of oysters used in diploid trials. Diploid trials were limited to 12 d, whereas triploid trials lasted up to 28 d. A longer trial duration for triploids may have led to exhaustion of metabolic reserves under non-feeding, anaerobic conditions leading to higher mortality rates and an associated decrease in the estimated LD<sub>50</sub>. Additionally, diploid oysters were collected from the wild and were larger (60–90 mm SH) than triploids (25–75 mm SH). Although physiological studies suggest that larger oysters are better suited to survive anoxic conditions due to larger capacity for carbohydrate storage, which is catabolized in anaerobic pathways (de Zwaan & Wijsman 1976), we detected no effects of oyster size on survival in either triploid or diploid trials. Overall, both diploid and triploid oysters were tolerant to partial burial and responded similarly to burial regardless of ploidy, which reaffirms the findings of a previous study on the lack of an effect of ploidy on oyster survival (Walton et al. 2013).

Oyster size did not have a significant effect on survival, which was unexpected. Under the anaerobic conditions of burial, oysters revert to catabolism of carbohydrates to maintain metabolic function (de Zwaan & Wijsman 1976). The ability of oysters to carry out anaerobic metabolism increases with developmental stage, as body size and the capacity for carbohydrate storage increases (Widdows et al. 1989); thus, we expected that juvenile oysters would experience higher mortality due to burial than adult oysters. Kranz (1974) also observed no size effects on survival for buried *C. virginica*, purple-hinge rock scallops (*Hinnites multirugosus*), which similarly adhere to hard surfaces, and bay scallops (*Aequipecten irradians*), whereas larger individuals of 2 mussel species (*Modiolus demissus* and *Mytilus edulis*) did survive better than smaller individuals. Others have documented effects of burial and anaerobic metabolism on juvenile *C. virginica* (16 mm SH, Widdows et al. 1989; 9–12 mm SH, Hinchey et al. 2006), but did not examine size effects. The fact that oysters in this study did not differ in survival suggests that neither the capacity for glycogen storage facili-

tated by larger body size nor the ability to physically ventilate the sediment to relieve sediment overburden were driving factors in survival.

Conversely, if we assume that oyster mortality increases significantly at burial depths >110% SH, then smaller oysters would experience significantly higher mortality at absolute sediment loads that would not affect larger oysters appreciably. For instance, a 6 mm sediment load should cause relatively low mortality (about 40%) in adult oysters of 100 mm SH (106% burial), whereas the same 6 mm load should cause 100% mortality in juvenile oysters ≤20 mm SH (≥130% burial). A major benefit of our findings is therefore that it will allow scaling of mortality rates of oysters as a function of sediment load and oyster size.

Epifaunal and infaunal species demonstrate varying degrees of tolerance to burial, based on their response to metabolic stress and life history strategy (Kranz 1974, Maurer et al. 1981, Hinchey et al. 2006). Motile infaunal bivalves are generally better suited than epifaunal bivalves to escape burial by vertical migration and siphon extension. Mortality of the infaunal bivalves *Mercenaria mercenaria* and *Nucula proxima* increased with burial depth and burial time (Maurer et al. 1981); however, *M. mercenaria* were able to overcome more than 16 cm of burial by vertical migration (Maurer et al. 1981). Epifaunal suspension feeders, such as oysters and mussels, are more susceptible to burial due to their sessile life history and lack of a digging foot (Kranz 1974, Hinchey et al. 2006). Overall, low mortality rates in the present study indicate that oysters are highly tolerant to partial and shallow total burial on weekly time scales, more so than other epifaunal suspension feeders (Maurer et al. 1981, Hinchey et al. 2006).

### Sublethal effects

Biodeposition was inversely related to partial burial depth. The sediment collected in the 110% treatment represented background deposition within the mesocosms, since oysters neither penetrated the sediment surface nor produced fecal pellets in that treatment. Similarly, no biodeposition was observed for juvenile oysters (9–12 mm SH) buried in 2–5 mm of silty sand (Hinchey et al. 2006). Biodeposition rates in 0–90% burial treatments were 1.4–3.4-fold greater than background sediment deposition (110%). Mean biodeposition in the unburied (0%) treatment (0.27 g DW d<sup>-1</sup>) was comparable to values in previous studies (0.1–0.2 g DW d<sup>-1</sup>; Haven & Morales-Alamo 1966,

1972). Although biodeposition was reduced in the 50 and 70% treatments ( $0.15\text{--}0.18\text{ g DW d}^{-1}$ ), it also fell within normal ranges of biodeposition for oysters not subjected to burial (Haven & Morales-Alamo 1966).

We did not observe significant effects of oyster size on biodeposition. In contrast, Haven & Morales-Alamo (1972) found that biodeposition rate increased asymptotically with oyster size, though the rate per unit weight of oyster decreased with increasing oyster size. The difference in response may be due to the different sizes of oysters used in the 2 studies, or due to our use of triploid oysters. Diploid oysters experience additional metabolic stress relative to triploids during spawning periods (Dégremont et al. 2012), and reproductive effort in oysters scales with oyster size (Thompson et al. 1996); therefore, diploid oysters are more likely to exhibit a size-specific response to external stressors than are triploids.

Biodeposition is a critically important process contributing to reef sustainability (DeAlteris 1988) and modulating sediment supply on and around reefs (Widdows et al. 1998). Oyster biodeposits are composed primarily of small inorganic particles with very slow settling velocities. The repackaging of these suspended sediments by oysters into feces and pseudofeces increases the settling velocity and cohesiveness of the sediment, leading to rapid deposition (Haven & Morales-Alamo 1966, 1972, DeAlteris 1988). In areas where bivalves occur, biodeposition accounts for as much as 25% of all deposition, and the rate of sediment delivery via biodeposition can be 8-fold higher than gravitational settling (Lund 1957a).

Long-term subtidal oyster reef persistence is determined by a balance between sediment accumulation, reef accretion, and sea level rise (DeAlteris 1988). Biodeposits contribute to reef accretion by filling reef interstitial space, effectively elevating the reef surface. Biogenic sediments (biodeposits and shell) on subtidal reefs accumulate as quickly as 50 cm per 100 y (DeAlteris 1988). Maximum sea level rise estimates for the mid-Atlantic region are 20–29 cm by 2100 (Sallenger et al. 2012), indicating that subtidal oyster reefs should outpace sea level rise given ideal conditions for accretion, similarly to intertidal reefs (Rodriguez et al. 2014). In the absence of biodeposits, caused either by reduced biodeposit production or erosion, reef accretion depends solely on the addition of shell through oyster recruitment and mortality, the rate of which may be less than the current rate of sea level rise (DeAlteris 1988). Intertidal reefs experience similar depositional events due to shifting sediments and storms (Taylor & Bushek 2008), but the effects of these events may be exacerbated by reduced erosion

due to lack of inundation, leading to further reductions in accretion on intertidal reefs relative to subtidal reefs. Thus, the reduction in biodeposit production associated with partial burial observed in this study suggests that non-catastrophic burial events can have lasting impacts on long-term oyster reef persistence even in the absence of mass mortality.

Condition index decreased significantly with increased burial depth. Oysters in the control treatment (0% burial) had the highest condition index, indicating a higher tissue-to-shell ratio in these oysters than those in other treatments. The decline in condition index with burial depth could be indicative of either the deterioration of tissue due to metabolic stress and sustained anaerobic conditions or to the investment of energy into shell growth when access to food and oxygen are limited by burial. In contrast, high suspended-sediment loads had little effect on oyster condition index after 7 d (Suedel et al. 2014), indicating that sediment deposition and burial are more detrimental to oyster condition index than are high suspended-sediment loads.

Shell growth was influenced by oyster size and burial treatment. Maximum growth rates were in the 110% burial treatment ( $0.32 \pm 0.05\text{ mm d}^{-1}$ ), which is higher than the growth rate for triploid *C. virginica* under normal conditions ( $0.2\text{ mm d}^{-1}$ ; Harding 2007). In addition, mean growth rates of the 70, 90, and 110% treatments ( $0.22\text{--}0.32\text{ mm d}^{-1}$ ) exceeded previously published growth rates ( $0.1\text{--}0.2\text{ mm d}^{-1}$ ) for both diploid and triploid *C. virginica* (Harding 2007, Kraeuter et al. 2007, Dégremont et al. 2012, Walton et al. 2013). Growth rates for the 0 and 50% burial treatments ( $0.12\text{--}0.16\text{ mm d}^{-1}$ ) agreed well with published estimates.

The effect of partial burial on oyster growth has not previously been addressed, but sediment deposition has been shown to negatively affect oyster growth (Grant et al. 1990, Lenihan 1999). Accelerated growth in shell height of oysters has been recorded in response to high-density conditions, which produces long and narrow oysters with shells up to 36 cm long (McCormick-Ray 2005). Under resource competition, oysters grow in the vertical axis to reach phytoplankton higher in the water column. Additionally, oysters in muddy habitats, which are often found almost completely buried, also exhibit an elongated shape, a presumed adaptation to rapidly accumulating soft sediments (Galtsoff & Luce 1930, Chinzei 1986). This life history may represent a trade-off by which oysters are subjected to enhanced sedimentation but avoid shell-boring polychaetes and sponges, which cannot survive anoxic sediments (Carver et al. 2010).

We suspect that oysters experiencing stress caused by partial or complete burial exhibit a similar vertical growth response to reach the sediment surface to feed and respire.

That the highest growth rate and lowest condition index were in the 110% treatment suggests that decreases in condition index were more likely due to oyster responses to burial than deterioration of tissues under anoxic conditions. We surmise that oysters responded to sediment burial by allocating energy reserves to shell growth in an attempt to remain above the sediment surface. This response would be comparable to vertical migration behavior by clams buried by sediment (Maurer et al. 1981). Seagrasses also exhibit a similar response, in which buried shoots increase vertical growth in response to moderate burial (Marbà & Duarte 1994, Cabaço et al. 2008). In oysters, this may represent a physiological response to accumulating biodeposits, in which oysters allocate resources to vertical growth. Oysters usually live in constant contact with biodeposits, which can accumulate rapidly and produce anoxic, reducing conditions similar to those below the sediment surface (Lund 1957b). The monotonic increase of growth rate with increasing burial suggests that this growth response was triggered before total burial and may serve as an important mechanism for oysters to outpace sediment accumulation. Growth rates were highest under complete burial, indicating that the likely limit to this increased growth is burial that induces mass mortality. Extrapolations from the estimated burial-survival function suggest that mass mortality occurs at approximately 130% burial.

The use of hatchery-reared triploid oysters in this experiment allowed for control of individual variation, but it precludes precise application of our observations of sublethal burial effects to wild, diploid oysters. Our results indicated no significant difference between triploid and diploid oysters with respect to survival. This may suggest that diploid oysters would respond similarly in sublethal effects, but previous studies indicate triploid oysters grow faster and have higher condition indices than diploid oysters under field conditions (Walton et al. 2013). Thus, our shell growth rates and condition indices are likely to overestimate those of diploid oysters (Walton et al. 2013), but we expect the observed trends to hold.

## CONCLUSIONS

The impacts of sediment deposition on estuarine habitats, particularly biogenic habitats, are expected

to increase with climate change. Amplification in storm frequency and intensity will increase the likelihood of mass transport of sediment that can cause rapid deposition events (Najjar et al. 2010). Increases in precipitation intensity are likely to mobilize stored sediments and magnify sediment inputs to estuaries (Meade 1982, Najjar et al. 2010), while sea-level rise will increase available accommodation space and enhance coastal erosion due to changes in estuary volume and tidal currents (Short & Neckles 1999). Sediment inputs affect water clarity, nutrient availability, and sediment characteristics, all of which impact species' distributions and estuarine productivity. Overall, the impacts of sediment deposition and burial on biogenic habitats are likely to increase over time, indicating that a clear understanding of the response of oyster reefs to short- and long-term burial events is needed.

The findings of our study can improve population model predictions by accounting for sublethal impacts of burial and episodic events that may impact reef persistence. These predictions may be used to inform reef placement or construction criteria to minimize adverse effects of partial burial on reef-building processes, particularly biodeposition. This study indicated that oysters can survive burial up to 70% of their shell height, but that sublethal effects of burial on biodeposition, growth, and condition index may occur at lower levels of partial burial. Oyster metabolic processes contribute to the growth of oyster reefs over time through reproduction, growth, and the production of biodeposits (DeAlteris 1988). These reef-building processes help maintain ideal reef conditions by elevating the reef off the bottom to heights where oysters experience reduced sedimentation, higher survival, and faster growth (Lenihan 1999). Understanding the impacts of sediment burial on oyster survival and function is critical to the success of continued restoration efforts, the recovery of natural oyster populations, and the productivity of aquaculture operations. This study demonstrates that burial of oysters by sediment, even partially, can impact the sustainability of natural and man-made oyster reefs by impairing reef-building processes.

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