Factors affecting recruitment, growth and survival of the eastern oyster *Crassostrea virginica* across an intertidal elevation gradient in southern New England

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ABSTRACT: Reef-building oysters are important coastal foundation species that provide ecosystem services. Overharvesting, destructive fishing practices, and environmental degradation have caused significant declines in global oyster populations, necessitating restoration efforts in many regions to rebuild oyster habitat and recover lost services. Understanding how biological and physical gradients regulate oyster recruitment, survivorship and growth will help guide future efforts to successfully restore oyster populations. We conducted a field experiment in Ipswich, Massachusetts, to quantify the effects of tidal elevation, predator exclusion, and reef vertical relief on oyster settlement, recruitment and survivorship. Oyster settlement was 3 times greater at the deepest intertidal elevation compared to the 2 shallower intertidal elevations. Reef vertical relief and predator exclusion did not affect oyster settlement or survivorship. Despite increased sedimentation and algal fouling with increasing depth, living oyster densities remained significantly elevated at the deepest intertidal elevation 8 mo after the experimental reefs were constructed. Oyster mortality during this period was highest (>70%) at our shallowest elevation treatment, likely the result of desiccation and food limitation. Meanwhile, mortality during the first winter post-recruitment was high across all elevations (all >64%), with our deepest elevation treatment experiencing the highest mortality rate (90%). Our results suggest that there is a gradient in oyster settlement rates, which increase at lower elevation, and that the dominant drivers of mortality also likely vary with elevation. Our findings highlight the need for region-specific studies to quantify biological and physical gradients prior to large-scale restoration efforts.

KEY WORDS: *Crassostrea virginica* · Oyster · Restoration · Biophysical gradients

1. INTRODUCTION

In marine and terrestrial systems, foundation species are recognized for having a disproportionately large role in facilitating associated faunal communities by creating complex habitats that ameliorate physical stress and provide refuge from predators and competitors (Dayton 1972, Angelini et al. 2011). Among marine foundation species, biogenic habitats such as seagrass beds, salt marshes, kelp beds, and coral and bivalve reefs provide valuable ecosystem services such as sediment stabilization (Fonseca 1996, Meyer et al. 1997, Wells et al. 2006, Gedan et al. 2011), nursery habitat of nekton (Beck et al. 2001, Heck et al. 2003, Minello et al. 2003), sequestration of carbon and nitrogen (Breaux et al. 1995, Herbert 1999, Mcleod et al. 2011, Smyth et al. 2013, Fodrie et al. 2017) and water filtration (Zu Ermgassen et al. 2012). Centuries of anthropogenic impacts on coastal and estuarine ecosystems have resulted in these systems being among the most degraded worldwide (Lotze et al. 2006, Worm et al. 2006).

The eastern oyster *Crassostrea virginica* has long been recognized for its direct fisheries value in the United States (Kirby 2004). In addition to their extractive value, oyster reefs provide a number of ecological services within coastal and estuarine systems. Oysters are capable of filtering large volumes of water and, thus influencing nutrient cycling and removing excess nutrients from estuarine systems (Newell et al. 2005, Piehler & Smyth 2011, Smyth et al. 2013). Newell & Koch (2004) found that oysters have a much higher weight-specific filtration rate and are present in higher densities than most other bivalve species, such as the hard clam *Mercinaria mercinaria*, and that oyster restoration has the potential to appreciably reduce turbidity in estuarine environments. Oyster reefs also provide structurally complex habitat in which numerous sessile and mobile organisms settle and find refuge (Wells 1961, Bahr & Lanier 1981, Lenihan et al. 2001). Furthermore, oyster reefs serve as foraging grounds for predators, increase landscape diversity, and can significantly reduce erosion and dissipate wave energy (Dame & Libes 1993, Meyer et al. 1997, Breitburg 1999, Grabowski 2004). Indeed, Grabowski et al. (2012) found that the ecosystem services provided by restored oyster reefs can far exceed their extractive value.

Primarily driven by overharvesting and destructive harvesting practices, it is estimated that 85% of oyster reefs have been lost globally (Zu Ermgassen et al. 2012). The pressure on oyster stocks from overfishing and destructive harvesting practices has been further compounded by environmental degradation, disease, and introduction of invasive species (Lenihan & Peterson 1998, Boesch et al. 2001, Kirby 2004, Kimbro et al. 2009). Oyster populations in the northeastern US have experienced centuries of intensifying pressure, beginning with commercial fishing dating back to the early 1600s (Kirby 2004). Having once impeded navigation in major coastal rivers such as the Charles River in Boston, MA (Wood 1865), oyster populations in the northeastern US are currently at less than 1% of their historical abundance and are categorized as functionally extinct (Beck et al. 2011). This degradation has resulted in almost complete forfeiture of the many ecosystem services derived from a once prevalent ecosystem engineer. The extent of oyster reef habitat loss experienced in the northeastern US suggests that oyster reef restoration will likely be necessary to rebuild reefs and recover lost ecosystem services (Beck et al. 2011). However, there are many potential barriers to successful restoration of biogenic habitats in the northeastern US; the present study aimed to enhance our understanding of how oysters are influenced by biotic and abiotic factors.

Despite increasing allocation of resources to oyster restoration efforts in recent years, the amount of restored oyster habitat still lags considerably behind other coastal biogenic habitats of similar restoration cost per area, such as salt marsh habitat (Grabowski et al. 2012). While restoration efforts that incorporate rigorous science into their methodology have provided invaluable insight into the factors influencing reef habitat recovery, much of this work has occurred on reefs in the Mid-Atlantic region of the US, the South Atlantic Bight and the Gulf of Mexico. For example, Schulte et al. (2009) found that oyster density was 4-fold greater on high-relief subtidal reefs than on low-relief subtidal reefs in the Chesapeake Bay. Similarly, Lenihan (1999) revealed that subtidal reefs in North Carolina with greater vertical relief experienced enhanced growth and reduced mortality on the reef crest compared to near the base and attributed these findings to taller reefs reducing exposure to hypoxic water by elevating oysters off the bottom. Fodrie et al. (2014) demonstrated that oyster settlement on restored reefs constructed along an intertidal to shallow subtidal elevation gradient was highest on the deepest reefs. However, this trend reversed after one year, potentially resulting from higher mortality on the deepest reefs where predation and biofouling are likely greatest.

While these studies have greatly enhanced our understanding of the factors that influence restoration success in the southeastern US, the relative contribution of abiotic and biotic factors to reef recovery and persistence in other regions may vary as a result of local processes. Moreover, our limited understanding of the factors that influence the recovery of restored intertidal reefs, particularly in the northeastern US, impedes optimal allocation of restoration resources (Kusler & Kentula 1989). Therefore, studies that quantify the effects of these factors on oyster restoration success are needed in regions such as the northeastern US, and aim to broaden our understanding by building on the rich conceptual foundation derived from oyster reef restoration research in the southeastern US.

To examine how biological (competition from other sessile crustaceans and gastropods, algal fouling, predator density) and physical (sedimentation, thermal stress) gradients influence reef evolution in a temperate estuary in the northeastern US, we experimentally evaluated how reef relief, predation risk, and aerial exposure frequency and duration affect oyster settlement, survivorship and growth. We

hypothesized that oyster settlement would be positively correlated with inundation time due to the greater period over which larvae could settle. Additionally, we hypothesized that emersion time at our highest intertidal elevation would create food limitation and reduce oyster growth compared to the 2 shallower intertidal elevations. Conversely, we hypothesized that predator exclusion effects would increase with depth (i.e. greater inundation period) as the major oyster predators in this system forage more efficiently in water, and intertidal excursions occur largely during periods of inundation.

2. MATERIALS AND METHODS

2.1. Study site

The Ipswich River Basin (42° 42′ N, 70° 49′ W) is approximately 40 km long and 6 km wide, encompassing a 400 km^2 area approximately 32 km to the north of Boston, MA, which discharges into the Atlantic Ocean through Plum Island Sound (Armstrong et al. 2001). Plum Island Sound estuary, which encompasses the Parker, Rowley, Eagle Hill and Ipswich Rivers and Plum Island Sound, is the largest wetland-dominated estuary in New England. These wetlands are comprised of a mosaic of interconnected habitats, which includes 3500 ha of salt marsh and relatively shallow soft-sediment habitats with a tidal amplitude of 2.6–3.6 m (Novak & Short 2012). Small populations of oysters are present in Plum Island Sound estuary and largely exist in loose shallow subtidal aggregations (Buchsbaum et al. 1998).

Two study sites in Eagle Hill River and 1 site in Ipswich River were identified using MassGIS (MassGIS 2002), Google Earth and field observations (Fig. 1). All 3 sites are intertidal with soft bottom bordered by *Spartina alterniflora* saltmarsh in the high intertidal and supratidal, and deeper central channels in the subtidal. The site in the Ipswich River is permanently closed to shellfish harvesting due to its proximity to a water treatment outflow; however, the water characteristics (temperature, nutrient loading, and salinity) of this site are not appreciably different from those in Eagle Hill River (Hopkinson et al. 1997). Water temperature data logged at 15 min intervals at both sites between November 2015 and May 2016 dif-fered on average by 0.7°C. Salinity, which was measured during each sampling event (range = 22–30), varied by less than 10% between sites during each sampling.

2.2. Experimental design

Oyster settlement units were created using dead oyster shells. Two different methods were used to construct experimental units that mimicked the high (patches of clumped oysters) and low (aggregations of individual unconsolidated oysters) relief oyster beds observed locally. Low-relief units emblematic of reefs with low densities of living oysters were created by drilling a hole near the umbo of weathered oyster shells and attaching them to a 0.25 m^2 piece of polyethylene mesh (9 × 9 mm openings) using cable ties so that shells lay flat with the more rugose outer shell facing upward. High-relief units mimicking reefs with greater densities of living oysters were created by embedding the same volume of oyster shells into a poured cement slab (0.25 m^2 × 2 cm deep), so that only the umbo was embedded and the remainder of the shell protruded vertically to ~15 cm above the sediment surface. High-relief units were constructed >30 d prior to their deployment to allow the cement bases to fully cure, as uncured cement is potentially toxic to some marine invertebrates. Predator exclusion cages (50 × 50 × 20 cm; l × w × h) were constructed from polyvinyl chloride coated wire mesh (5.7 mm^2 openings, 0.6 mm wire diameter). Caging material of this size effectively excludes predators so that oyster recruitment can be quantified in the absence of predation (Pardo et al. 2007). Full cages consisted of a top, bottom and all 4 sides. Cage controls consisted of a top, bottom and 2 parallel sides,
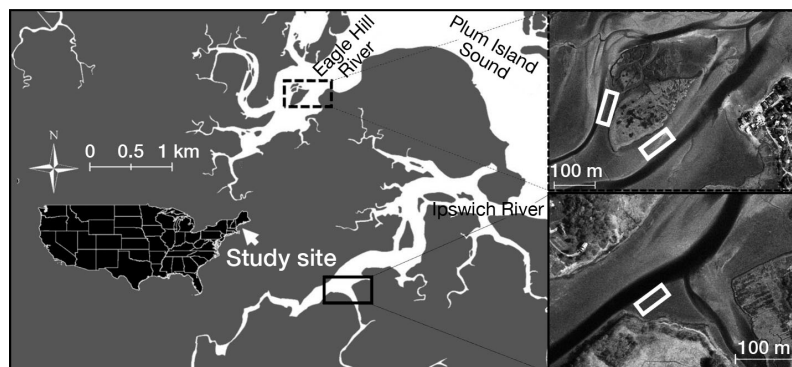

Fig. 1. Study sites in Ipswich, Massachusetts. The upper right image shows the 2 replicate sites in Eagle Hill River where settlement units were deployed. The lower right image shows the site in Ipswich River where settlement units were deployed

with the other 2 sides open. Open (control) treatments did not receive any cage panels. Relief treatments (high, low) were fully orthogonally crossed with predator exclusion (full cage, cage control, open), yielding 6 individual treatment combinations, each with 3 replicates. Stainless-steel stakes attached with cable ties were used to secure all treatments to the sediment. At each of the 3 sites, settlement units were positioned at 3 elevation treatments: low (+0.0 m relative to mean low low water [MLLW]); intermediate (+0.5 m MLLW); and high (+1.0 m MLLW).

To sample epifaunal community characteristics across an elevation gradient without disturbing natural processes on settlement units between semi-annual sampling events, such as sedimentation and algal fouling, we created separate epifaunal sampling trays (50 × 50 × 10 cm). Each tray was comprised of a base and 4 sides, but without a top, using polyvinyl chloride coated wire mesh (5.7 mm² openings, 0.6 mm wire diameter). Epifaunal sampling trays were filled with 19 l of weathered oyster shells and secured to the underlying sediment using stainless-steel stakes. Epifaunal trays were sampled monthly between June and November of 2015. Two replicate epifaunal sampling trays were positioned at each elevation across all sites beginning in May. Sampling was conducted to measure epifaunal settlement, sedimentation, algal cover and predator abundance. Epifaunal trays were emptied and rinsed into 0.25 m² box sieves with 500 µm mesh. Oyster shells were returned to the sampling tray, the tray was replaced at the site, and the remaining sieve contents were bagged and returned to the lab. Sieved samples were sorted, and animals were retained for meristic identification and quantification.

Settlement units at the 2 shallowest intertidal depths were exposed during almost every low tide, while units at the deepest intertidal depth were frequently inundated for the entire duration of neap tidal cycles. Exposure periods over a tidal cycle (mean and range) were obtained from local water-level data: +0.0 m MLLW = 3.6% (0.0–10.8%) exposure; +0.5 m MLLW= 19.6% (2.5–30.0%) exposure; +1.0 m MLLW = 36.3% (26.6–45.0%) exposure. Settlement units were deployed in April 2015, prior to the peak period of oyster spawning in Massachusetts, which generally occurs in the late summer through early fall (Sellers & Stanley 1984). Treatments were randomly assigned along horizontal transects at each elevation treatment and separated by at least 3 m.

Total sedimentation was quantified by measuring sediment depth at the center of the settlement units to the nearest millimeter. Sediment depth was measured from the sediment surface to the top side of the cement or polyethylene mesh bases to which oysters were affixed. Algal percent cover was quantified using 0.25 m² point-intercept quadrats with 25 points per quadrat. Predator abundance sampling was conducted monthly across all sites and elevations using unbaited, collapsible minnow traps (22.9 × 44.5 cm, 2.5 cm openings, 0.6 cm mesh, N = 2) and crab traps (66 × 48.3 × 22.9 cm, 15.2 cm openings, 1.0 cm mesh, N = 2) placed directly on the bottom, randomly interspersed among settlement units. Traps were deployed during an evening low tide and retrieved the following morning, resulting in an average deployment of approximately 12 h. Upon retrieval of the traps, all fishes and crustaceans were bagged and returned to the lab to be identified to species level, counted, measured to the nearest millimeter, and weighed. Catch was standardized to catch per unit effort by species (CPUE, count and biomass [g] per 12 h).

Sessile organism densities were quantified in November 2015 and April 2016 by collecting a representative sample of oyster shell substrate (~25 oyster shells per unit: 5 along each edge and 5 from the center) by hand from all settlement units. The collected shells were placed in bags and returned to the lab. Counts and length measurements of living and dead sessile organisms were recorded from the tops (rough outside) and bottoms (smooth inner surface) of oyster shells and averaged. Individuals were considered dead if the body cavity was devoid of living tissue. Visible marks or 'scars' indicating recently settled oysters and barnacles were counted but lengths were not measured. Oyster and barnacle scars were differentiated by their morphology. Specifically, barnacle scars are typically round with striations radiating from the center, while oyster scars are smooth and irregularly shaped (Anderson & Connell 1999). Species-specific mortality was calculated as the percentage of dead individuals and scars relative to the sum of living individuals, dead individuals, and scar counts. The sum of living, dead and oyster scar counts was also used as a measurement of oyster settlement.

To standardize for shell area sampled, oyster shell samples were photographed over a gridded background and photographs were analyzed to quantify surface area using ImageJ image analysis software (Rasband 1997). Temperature loggers (HOBO TidbiT, Onset) were affixed to 1 settlement unit at each elevation across all sites in November 2015 to monitor temperatures experienced at each tidal elevation.

In June 2016, we deployed a follow-up experiment to directly examine predation intensity across eleva-

tions. Experimental units were created by securing 7 hatchery-raised oysters (range = 6–12 mm) obtained from Roger Williams University hatchery to concrete paving tiles (15 × 15 × 4 cm) using cyanoacrylate. Tiles were randomly assigned to 1 of 2 treatments: 'caged' or 'open'. Cages, which were 15 × 15 × 10 cm in size, were constructed from polyvinyl chloride coated wire mesh (5.7 mm^2 openings, 0.6 mm wire diameter). Full cages were intended to exclude all fish, crab and gastropod predators and consisted of a top, bottom and 4 sides. Open cages consisted of a bottom, 3 sides and a top that covered half of the cage. Open cages were intended to allow access by all predators while at the same time accounting for caging effects on flow.

Five replicates of each cage treatment were placed at least 3 m apart at each of 3 elevation treatments: +0.0 m, +0.5 m, and +1.0 m MLLW. This design was also replicated across the 3 sites. Tiles were secured within cages using cable ties to prevent tiles from moving within cages and dislodging of oysters. All cage-tile units were affixed directly to the sediment using 4 sections of metal conduit tubing secured to the corners of the cages. Cages were deployed at low tide, and we returned after 1, 3 and 30 d to quantify mortality. Predation mortality was calculated by counting the number of dead oyster that had broken shells or those that were completely missing. Gaping oysters and those missing 1 half by a clean separation at the hinge were recorded as natural (non-predation related) mortality.

2.3. Data analysis

We used linear mixed effects models to analyze the effects of elevation (low, intermediate, high), relief (low and high), and predator exclusion (full cage, cage control, open) on sedimentation, algal cover, counts of sessile organisms, lengths of sessile organisms and percent mortality of sessile organisms. Additionally, we tested the effect of elevation and month on predator catch per unit effort (count and biomass) and density from trapping and epifaunal sampling tray data, respectively. Site was included as a random factor in these models. We used R version 3.2.5 (R Core Team 2015) and the package 'lme4' (Bates et al. 2014) to conduct mixed effects analyses.

For our analysis of sessile organism counts, size and percent mortality, we tested the effects of elevation, substrate relief and predator exclusion treatment as fixed factors and site as a random factor. Separate analyses were conducted for data collected in November 2015, at the end of the first growing season post-settlement, and in April 2016, after the first winter. For our analysis of algal cover and sedimentation, we included elevation, substrate relief, predator exclusion and month as fixed factors, and site as a random factor. In addition, we analyzed the effects of elevation and month (fixed factors) and site (random factor) on trapping and epifaunal tray predator data. Potential biases associated with temporal autocorrelation in our time series data were addressed by incorporating an autocorrelation structure with a continuous time covariate, function 'corCAR1' (Box et al. 2013), into our mixed effects models. Post-hoc multiple comparisons were conducted using the 'multcomp' procedure for significant effects (Hothorn et al. 2013). This approach conducts simultaneous tests and calculates confidence intervals for mixed effects models using an asymptotic multivariate normal distribution (Bretz et al. 2010).

Next, we tested for correlation between oyster densities (oysters 200 cm^{-2}) and sediment depth (mm), algal fouling (% cover), and barnacle densities (barnacles 200 cm^{-2}) separately. Data were tested for normality with the Shapiro-Wilk test prior to regression analysis. Data that satisfied the assumption of normality were analyzed using a Pearson correlation test. Those that failed to meet the assumption of normality were analyzed using Spearman's rank order correlation. We used classification and regression tree (CART) analysis to evaluate which factors were the most powerful in explaining post-settlement oyster mortality. Classification and regression trees explain variation in a single response variable using multiple explanatory variables to partition the data into increasingly homogeneous groups. Trees were constructed by repeatedly splitting the data based on a single explanatory variable at each split. At each split in the tree, the data were partitioned into 2 mutually exclusive groups within which the data were as homogeneous as possible. Trees were grown using a recursive partitioning 'rpart' function from package 'rpart' with a threshold of p < 0.05 (Therneau et al. 2010). The classification and regression tree analysis for oyster mortality considered 8 independent variables: elevation, cage treatment, relief, *S. balanoides* density, *C. fornicata* density, and seasonal averages of algal cover, sedimentation, and *C. maenas* CPUE. Over-fitted trees were pruned to optimal size using v-fold cross-validation.

Linear mixed effects models were used to analyze the effects of elevation (low, intermediate, high) and predator exclusion (full cage, open cage) on oyster

mortality on the experimental predation tiles. Each sampling time point was analyzed separately.

3. RESULTS

Oyster settlement was significantly affected by elevation ($F_{2,38}$ = 11.85, p < 0.001; Fig. 2A), but was not influenced by relief or predation. Settlement density at the deepest elevation, +0.0 m MLLW, ($\mu \pm 1$ SE: 6.73 ± 1.44 oysters 200 cm^{-2}, or 336.5 oysters m^{-2}) was significantly greater than at either +0.5 m (1.84 ± 0.54 oysters 200 cm^{-2}, or 92.0 oysters m^{-2}) or +1.0 m (0.94 ± 0.49 oysters 200 cm^{-2}, or 47.0 oysters m^{-2}), which did not differ from one another (Fig. 2A). Elevation also significantly affected percent algal cover on settlement units in 2015 ($F_{2,106}$ = 149.10, p < 0.001; Fig. 3A). Algal cover, which was comprised predominantly of *Ulva* spp., was significantly greater at +0.0 m (33.02 ± 2.04 %) than at either +0.5 m (6.30 ± 0.93 %) or +1.0 m (0.60 ± 0.26 %), which were not significantly different from each other. Elevation of settlement units also significantly affected the densities of 2 other sessile invertebrate species, the acorn barnacle *Semibalanus balanoides* ($F_{2,51}$ = 11.15, p < 0.001; Fig. 3B) and the slipper limpet *Crepidula fornicata* ($F_{2,51}$ = 7.39, p = 0.002; Fig. 3C). Densities of *S. balanoides* were nearly 800 % greater at +0.0 m (78.69 ± 23.88 barnacles 200 cm^{-2}) than at +0.5 m (10.10 ± 4.05 barnacles 200 cm^{-2}) and nearly 4500 % greater than at +1.0 m (1.77 ± 1.01 barnacles 200 cm^{-2}). *C. fornicata* densities were over 3000 % greater at +0.0 m (0.68 ± 0.25 limpets 200 cm^{-2}) than at +0.5 m (0.02 ± 0.02 limpets 200 cm^{-2}), with no limpet presence at +1.0 m (0.00 ± 0.00 limpets 200 cm^{-2}). Oyster settlement was positively correlated with percent algal cover (Spearman's correlation, r_s = 0.51, p < 0.001), *S. balanoides* density (r_s = 0.73, p < 0.001) and *C. fornicata* density (r_s = 0.57, p < 0.001).

Similar to the pattern observed for oyster settlement, living oyster densities in November 2015 were significantly different among elevation treatments ($F_{2,36}$ = 14.39, p < 0.001; Fig. 2B), but were not affected by habitat relief or predation risk. Living oyster densities were more than 3 times greater at the deepest elevation, +0.0 m (6.29 ± 1.33 oysters 200 cm^{-2}, or 314.50 oysters m^{-2}), than at either +0.5 m (1.53 ± 0.45 oysters 200 cm^{-2}, or 76.50 oysters m^{-2}) or +1.0 m MLLW (0.44 ± 0.37 oysters 200 cm^{-2}, or 22.00 oysters m^{-2}). The size of living oysters in November 2015 ($\mu \pm 1$ SE: 6.21 ± 0.65 mm shell height) was not significantly different among elevation, relief, or predator exclusion treatments (Fig. 2C).
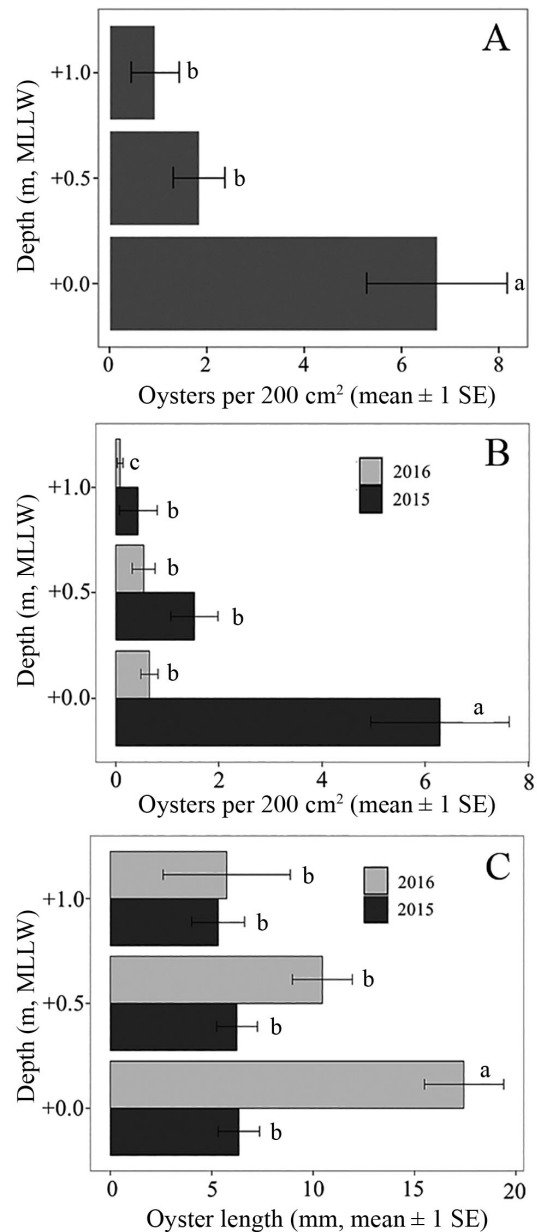

Fig. 2. Oyster settlement. (A) The sum of oyster scars and living and dead oysters in November 2015. (B) Living oyster density and (C) length in November 2015 (black) and April 2016 (gray). Data are shown as mean ± 1 SE. Significant differences (α = 0.05) between treatments are represented by different letters at the right of the bars. MLLW: mean low low water

Between April and November 2015, sedimentation was consistently greater on settlement units at deeper intertidal elevations ($F_{2,95}$ = 21.82, p < 0.001). Generally, we observed a pattern of high-to-low sedimentation from deep-to-shallow elevation treatments; however, there was a significant elevation-predator exclusion interaction ($F_{4,95}$ = 3.77, p = 0.007;
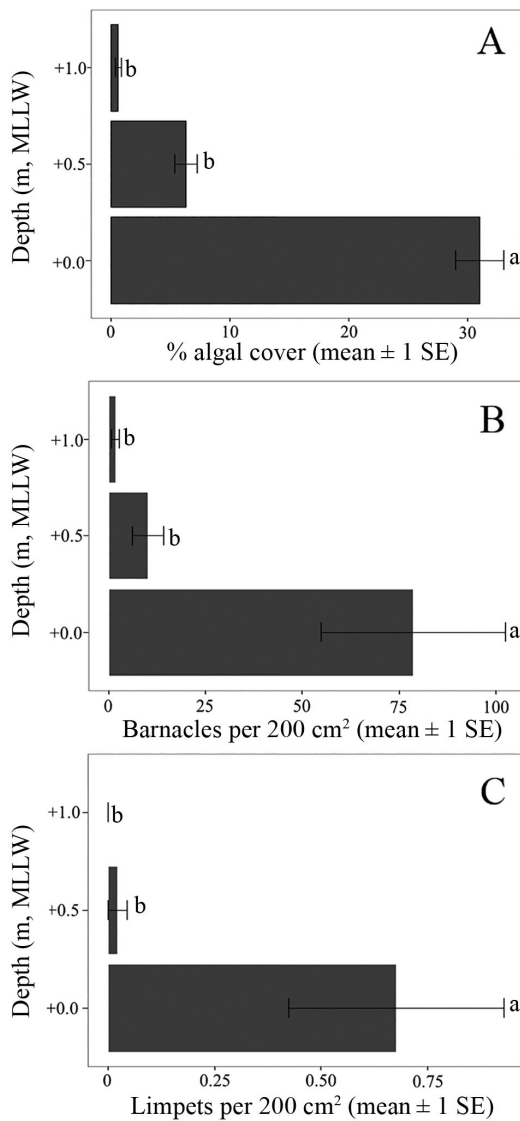
Fig. 3. (A) Percent algal cover averaged across months between April and November 2015, (B) barnacle density in November 2015, and (C) limpet density in November 2015. Data are shown as mean ± 1 SE. Significant differences (α = 0.05) between treatments are represented by different letters at the right of the bars. MLLW: mean low low water

Fig. 4. Sediment depth (A) averaged across months between April and November 2015, and (B) in April 2016. Data are shown as mean ± 1 SE. Significant differences (α = 0.05) between treatments are represented by different letters at the right of the bars. MLLW: mean low low water

Fig. 4A). For all months, sedimentation rates were greater in full cage and cage control than in open plots at our deepest elevation, +0.0 m, where sedimentation was generally greatest (Fig. 4A). Averaged across months, sediment depth overlying settlement units at +0.0 m was greater on full cage (43.50 ± 6.97 mm) and cage control (33.61 ± 5.86 mm) than open (13.61 ± 3.15 mm) treatments (Fig. 5A). A similar, although non-significant, trend was observed at our intermediate elevation: full cage: 14.72 ± 4.74 mm; cage control 21.11 ± 6.81 mm; open: 6.53 ± 2.45 mm
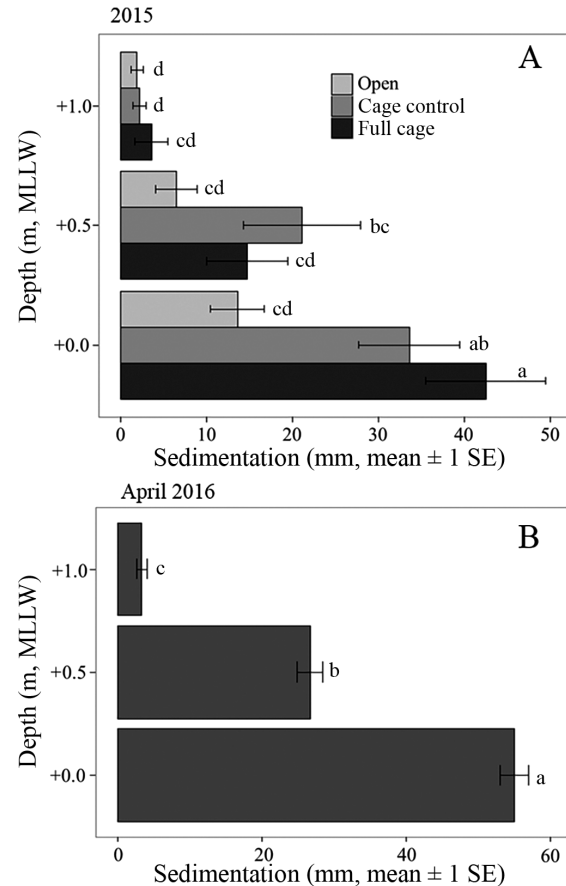
(Fig. 4A). Oyster settlement density was positively correlated with sedimentation rates (r_s = 0.31, p = 0.020).

Between the time of settlement and our November 2015 monitoring, oyster mortality was significantly affected by settlement unit elevation. Percent mortality on settlement units at the 2 deeper elevation treatments, +0.0 m and +0.5 m, were relatively low and not significantly different from one another at 11.5 ± 6.1% and 11.1 ± 5.1%, respectively. However, at our highest elevation treatment, oyster mortality (63.9 ± 17.7%) was significantly greater than at either of the 2 treatments with less aerial exposure ($F_{2,22}$ = 28.99, p < 0.001). Classification and regression tree analysis, which identified the factor(s) that were most important in determining early oyster mortality, indicated that elevation was the most powerful predictor of oyster mortality, partitioning +0.0 m and +0.5 m into one node (mean mortality = 11.32%) and +1.0 m into a separate node (mean mortality = 63.89%; Fig. 5).
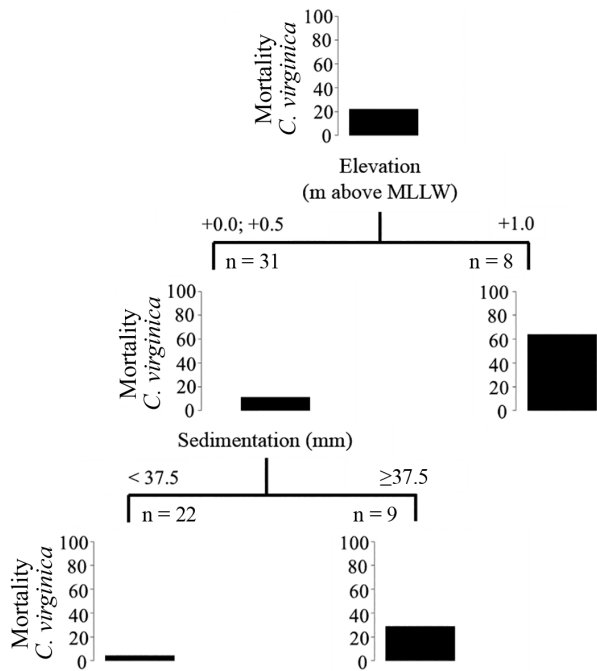
Fig. 5. Classification and regression tree for mean oyster mortality between settlement and November 2015. Branches represent statistically significant splits at α = 0.05

Within the +0.0 m and +0.5 m, low mortality node, the most powerful splitting factor was sedimentation, with units subjected to less than 37.5 mm of sedimentation experiencing significantly lower mortality (mean mortality = 4.16%) than those with >37.5 mm of sedimentation (mean mortality = 28.81%; Fig. 5).

The European green crab *Carcinus maenas* accounted for over 99% of the potential oyster predators we captured in the crab and minnow traps. Predator sampling in 2015 revealed no effect of elevation on *C. maenas* abundance (CPUE, crabs trap^{-1} 12-h-soak^{-1}) or biomass (g trap^{-1} 12-h-soak^{-1}). A temporal pattern of increasing *C. maenas* CPUE from early summer (May: 1.44 ± 0.56 [SE] crabs trap^{-1} 12-h-soak^{-1}) to late fall (October: 9.89 ± 2.13 crabs trap^{-1} 12-h-soak^{-1}) was observed ($F_{3,15}$ = 5.80, p = 0.008). Panopeidae mud crabs and juvenile *C. maenas* comprised the vast majority of the potential oyster predators found in epifaunal trays. Elevation did not significantly influence CPUE of either mud crabs or *C. maenas* in epifaunal trays; however, density of *C. maenas* juveniles was higher in the early summer than fall, whereas mud crab density increased from summer into fall.

Temperature was highly variable throughout the winter. Below-freezing temperatures were observed frequently throughout the winter at all elevations, reaching minimum temperatures during February. Minimum winter temperatures of −18.1°C, −17.9°C and −12.3°C were experienced at +1.0 m, +0.5 m, +0.0 m, respectively. Elevation did not significantly affect mean daily temperature between January and the beginning of May 2016. Elevation did, however, have a significant effect on daily temperature range ($F_{2,294}$ = 16.25, p < 0.001). Mean daily temperature range at the deepest elevation (+0.0 m; 9.62 ± 0.42 [SE] °C) was significantly lower than at both intermediate (+0.5 m; 12.53 ± 0.53°C) and high (+1.0 m; 13.85 ± 0.60°C) elevations. Mean daily temperature range did not differ significantly between intermediate and high elevation treatments.

By April 2016, the number of living oysters had decreased across all elevation treatments. We observed a significant elevation by year interaction in living oyster density ($F_{2,72}$ = 11.23, p < 0.001; Fig. 2B). Despite appreciable declines in oyster density across all elevations in 2016, there remained a significant effect of elevation on living oyster density ($F_{2,34}$ = 3.63, p = 0.037). Densities of living oysters at +0.0 m (0.65 ± 0.17 oysters 200 cm^{-2}, or 32.5 oysters m^{-2}) and +0.5 m (0.55 ± 0.22 oysters 200 cm^{-2}, or 27.5 oysters m^{-2}) were significantly greater than that at +1.0 m (0.09 ± 0.06 oysters 200 cm^{-2}, 4.5 oysters m^{-2}). Between November 2015 and April 2016, we observed decreases of 89.7%, 64.1% and 79.5% in living oyster density at +0.0 m, +0.5 m, and +1.0 m, respectively. Relief and predator exclusion treatments did not significantly affect living oyster density in 2016. Among the surviving oysters, elevation significantly affected oyster length ($F_{2,22}$ = 7.115, p = 0.004): Oyster lengths at +0.0 m (17.43 ± 1.96 mm) were significantly greater than those at either +0.5 m (10.45 ± 1.47 mm) or +1.0 m (5.75 ± 3.12 mm), which were not significantly different from one another (Fig. 2C). Sedimentation increased significantly with greater depth ($F_{2,34}$ = 349.51, p < 0.001; Fig. 4B), but was not affected by predation risk or habitat relief. Sedimentation at +0.0 m (55.00 ± 1.98 mm) had completely covered almost all settlement units regardless of relief treatment, while sedimentation at +0.5 m (26.67 ± 1.81 mm) generally covered the entirety of low-relief treatments, but left portions of high-relief treatments exposed (Fig. 4B). Sedimentation at +1.0 m (3.33 ± 1.98 mm) was low on both low and high-relief units (Fig. 4B). Algal cover on +1.0 m settlement units was largely absent (1.20 ± 0.32%), and there was no algal cover at +0.0 m and +0.5 m.

Results from our supplementary predation experiment indicated high predation rates within 30 d of deployment. Natural mortality was absent in all pred-

ator exclusion treatments after 24 and 72 h (Fig. 6). We observed a significant elevation × cage interaction on mortality at 24 h ($F_{2,46}$ = 3.838, p = 0.029). Open cage mortality at 24 h was significantly higher at +0.5 m (μ ± 1 SE: 23.8 ± 6.7%) than at +1.0 m (3.2 ± 2.1%), but neither were significantly different from +0.0 m (12.7 ± 6.0%). Similarly, we observed a significant elevation × cage interaction on mortality at 72 h ($F_{2,48}$ = 7.692, p = 0.001; Fig. 6). Cumulative open cage mortality at 72 h was significantly higher at +0.0 m (28.6 ± 5.8%) and +0.5 m (28.6 ± 5.8%) than +1.0 m (4.8 ± 2.4%). Significant elevation ($F_{2,46}$ = 6.412, p = 0.003) and cage ($F_{2,45}$ = 126.263, p < 0.001) effects on cumulative mortality were detected in our 30 d sampling data (Fig. 6). Cumulative mortality in the closed treatments was not significantly different among +0.0 m (7.94 ± 3.46%), +0.5 m (3.17 ± 2.10%) and +1.0 m (25.40 ± 10.03%). Among open cage treatments, cumulative mortality after 30 d was significantly higher at +1.0 m (84.13 ± 5.56%) than at +0.0 m (57.14 ± 5.83%), but neither were significantly different from +0.5 m (73.01 ± 8.40%; Fig. 6).

4. DISCUSSION

Among the most basic necessities for successful oyster restoration is the knowledge of adequate re-

Fig. 6. Cumulative mortality of juvenile oysters on tiles as a function of cage treatment, elevation and sampling interval. Data are shown as mean ± 1 SE. Significant differences (α = 0.05) between cage and elevation treatments are represented by different letters at the right of the bars. Post-hoc letters are specific to the individual time interval. MLLW: mean low low water

cruitment rates of oysters (Coen & Luckenbach 2000). We demonstrated that settlement of oyster spat, as well as settlement rates of other numerically dominant sessile organisms, were negatively correlated with tidal emergence in our study system. Previous studies on vertical settlement patterns of oysters in the northeastern US, while limited, have demonstrated that gradients can vary at regional and even estuarine scales. For example, Prytherch (1929) found that in Milford Harbor, CT, oyster settlement occurred from the bottom of the channel up to +0.6 m above MLLW, but that the greatest settlement occurred between −0.3 m and +0.3 m relative to MLLW. In contrast, Galtsoff et al. (1930) found that in Onset Harbor, Wareham, MA, only ~200 km northeast of Milford Harbor and ~100 km south of our study site, oyster larvae settled from below MLLW up to +1.0 m, with peak settlement densities occurring between +0.5 m and +0.6 m relative to MLLW. Kenny et al. (1990) demonstrated that oyster recruitment is not always directly correlated to emersion period; for instance, it may be influenced by stratification of larvae in the water column (Carriker 1951), flow speed (Jonsson et al. 1991), and fouling communities (Osman et al. 1989). Similar variability in oyster settlement gradients occurs in the Mid-Atlantic and southeast regions of the USA over spatial scales of 10s to 100s of kilometers (Loosanoff 1933, McDougall 1943, Bartol & Mann 1997, Fodrie et al. 2014). Although our findings suggest a positive correlation between depth and oyster settlement, we sampled discrete tidal elevations. Thus, it is possible that peak settlement occurred in the interval between our elevation treatments.

Settled oysters face many physical and biological stressors that they must overcome to survive past early life stages. Fodrie et al. (2014) suggested that vertical gradients in predation, competition, and disturbance, which are well established paradigms in salt marsh (Pennings & Bertness 2001) and rocky shore (Dayton 1971) ecosystems, may be similarly applicable to shellfish reefs. The pronounced mortality of settled oysters at our highest elevation treatment (+1.0 m MLLW) was likely driven by exposure-related stress, as these oysters were subjected to less sedimentation and potential competition, and expe-
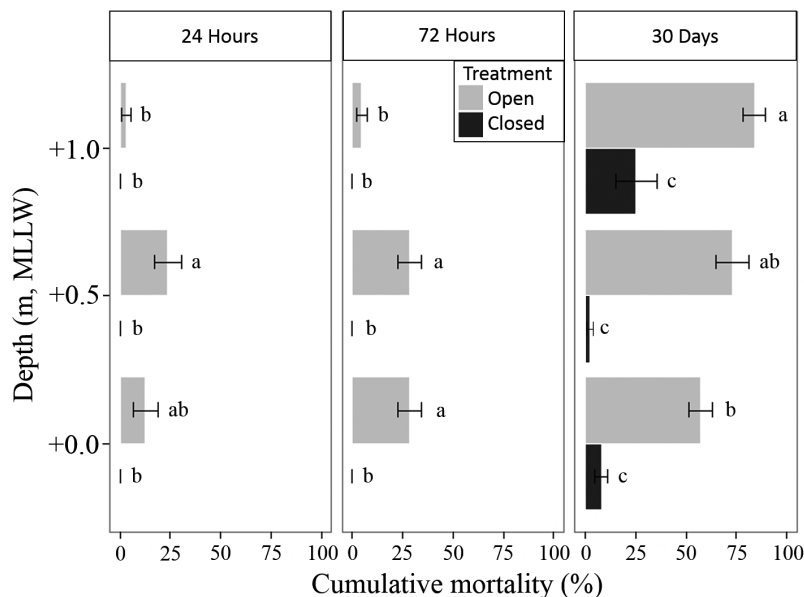
rienced similar predator densities as those at our 2 deeper treatments. The effects of excessive exposure resulting in desiccation and food limitation often mediate the upper vertical limits of intertidal organisms, including oysters (Michener & Kenny 1991, Kingsley-Smith & Luckenbach 2008). Given the multitude of interacting factors that contribute to stress from aerial exposure, the exposure duration that results in the highest oyster survival varies considerably among studies. For example, while Ridge et al. (2015) found an upper growth boundary of 55% aerial exposure, Roegner & Mann (1995) found that during a particularly high temperature period, complete mortality was observed at elevations corresponding to >25% aerial exposure. The significantly elevated mortality rates of early post-settlement oysters at our high emersion compared to our intermediate emersion treatment suggest a precipitous increase in lethal effects of aerial exposure resulting from the ~17% greater emersion from moving +0.5 m higher in the intertidal. Conversely, a similar difference in tidal emersion between our 2 deeper treatments did not significantly affect early-post settlement mortality rates. However, sub-lethal effects of greater emersion between these 2 treatments were apparent by April 2016 and manifested as reduced growth.

Effects of emersion duration on oyster size were not observed in November 2015, but by April 2016, surviving oysters were significantly larger at the deepest treatment relative to either of the 2 shallower treatments (Fig. 2C). Differences in mean length could have resulted from disproportionate mortality of larger size-class oyster at mid and high intertidal reefs or as a result of slower growth rates with increasing aerial exposure, a consequence of increased metabolic stress (Dame 1972) and reduced feeding time (Peterson & Black 1987). Previous studies have found an inverse relationship between aerial exposure and bivalve growth rates, suggesting a potential mechanism for the gradient in oyster sizes across the depth range observed in this study (Peterson & Black 1988, Bartol et al. 1999). Moreover, the seasonal effect of elevation on oyster growth that we documented is consistent with findings by Roegner & Mann (1995), who noted greater growth disparity among elevations in spring relative to summer or fall.

Densities of the potential competitors *S. balanoides* and *C. fornicata* were greatest at our deepest sites (Fig. 3B,C). Although *S. balanoides* significantly outnumbered oyster settlers, oysters typically settle later in the year (Sellers & Stanley 1984, Kordas &

Dudgeon 2009), and we found numerous instances of oysters settling on top of juvenile barnacles. These findings are in agreement with previous studies suggesting that settling oyster may not differentiate between the calcareous surfaces of barnacles and other hard substrata (Osman & Whitlatch 1995), and that oyster settlement may actually be positively correlated with the presence of living barnacles (Osman et al. 1989). It has been postulated that the topographic relief added by barnacle presence may increase contact of oyster larvae with the substrate surface by disrupting the boundary layer, thereby enhancing settlement (Osman et al. 1989). Algal cover was similarly greatest at our deepest elevation treatment and decreased with increasing aerial exposure (Fig. 3A). It is possible that the presence of algal turf at our deepest elevation treatment may have inhibited settlement to a degree, as suggested by Ortega & Sutherland (1992) as well as Thomsen & McGlathery (2006); however, as algal coverage averaged ~30% at +0.0 m, we suspect oyster larvae were not encountering the dense algal mats (>2 kg wet weight m^{-2}; Thomsen & McGlathery 2006) described in studies where macroalgal mats have created physical barriers to settlement.

That predation risk did not affect post-settlement mortality of naturally settled oysters may be explained by several factors. While it is possible that predation by crustacean and gastropod predators may not influence post-settlement mortality of oysters in our system, predation rates on juvenile oysters by a major crab predator have been found to correlate positively with recruit density (Eggleston 1990). Specifically, Eggleston (1990) found absence of predation on oysters by blue crabs *Callinectes sapidus* below some low prey threshold, characteristic of a 'displaced' type II functional response. While invasive species, such as green crabs, are often characterized by their ability to rapidly and more efficiently exploit resources than native species (Vitousek et al. 1990, Strayer et al. 2006), green crabs, the major bivalve predator in our study system, have significantly increased their per capita predation rates on bivalves with increasing density (Walton et al. 2002). Thus, recruitment to our units may have been too low to result in significant predation (Brown & Swearingen 1998, Knights et al. 2012). Alternatively, if oyster predators such as flatworms and small oyster drills, which were below the size excluded by our mesh, were the dominant predators in our system, our predator exclusion treatment would have failed to remove their effects on mortality. Yet, neither were observed in our epi-

faunal sampling trays or on our settlement units, suggesting that they are not major sources of oyster mortality in northern Massachusetts.

Contrary to our first experiment where there was no effect of predation risk, results from our supplementary oyster predation experiment suggest that predation was important in our system and could impede oyster reef restoration efforts. Within 72 h of deployment, predators had consumed nearly 30% of oysters in open cages at our 2 deepest elevations (Fig. 6). In contrast, open cages at +1.0 m experienced less than 5% predator mortality during the first 72 h. These findings may reflect increased foraging efficiency of crab predators on oysters that are mostly submerged, a finding supported by previous studies that have demonstrated a positive correlation between predation and depth (Nichy & Menzel 1967, Johnson & Smee 2014). However, cumulative mortality was higher at +1.0 m than at +0.0 m after 30 d (Fig. 6), which likely stemmed from the fact that sediments had started to accumulate after 30 d on oyster tiles at +0.0 m and +0.5 m, reducing predator access to these oysters, but likely inducing mortality.

We hypothesize that the difference in predator treatment observed between the natural recruitment and stocked oyster experiments could have resulted from differential access by predators. Naturally recruited oysters did not reach sizes approaching the hatchery reared oysters until November, by which time sedimentation and algae-covered settlement units at our 2 lower elevations likely already obscured oysters from easy detection by predations, particularly in low-relief treatments. While the potential for sedimentation to reduce foraging efficiency may have been of lesser importance on high-relief treatments, the greater structural complexity of these units may have inherently limited access by larger predators. Although sedimentation was considerably lower at our highest intertidal elevation, oyster densities were considerably lower than those on our stocked tiles, and the difference in percent mortality between the 2 experiments may be attributable to a density-dependent response of predators (Seitz et al. 2001). Thus, our results suggest that predation could represent a considerable source of juvenile mortality in this system, but its intensity is likely modified by bio-physical gradients and density-dependent effects.

Elevated levels of allogenic sedimentation have the potential to hinder reef accretion processes by reducing settlement, survival and growth of oysters (Thomsen & McGlathery 2006, Kimbro et al. 2014). Indeed, in a study from Delaware Bay, Taylor & Bushek (2008) found that shifting sediment may be more important in limiting development of oyster reefs than predation, ice shear or disease. Although sedimentation was found to be positively correlated with oyster settlement, likely due to some unquantified metrics such as elevated flow resulting in greater sedimentation and oyster settlement, our results suggest that sedimentation was a major contributor to post-settlement mortality of oysters. Classification and regression tree analysis indicated that sedimentation was highly correlated with post-settlement mortality during summer and fall 2015. Across our 2 deeper treatments, sedimentation was the most powerful predictor of post-settlement mortality, with the high sedimentation group experiencing nearly 7-fold greater mortality than that of the low sedimentation group (Fig. 4). Moreover, sedimentation appeared to be the primary cause of over-winter mortality across our mid-level and deep units, accumulating to depths covering nearly all units at +0.0 and +0.5 m MLLW regardless of substrate relief treatment.

Based solely on year-one recruitment, in the studied system the low intertidal would appear to be the optimal elevation for future restoration; however, physical stress from sedimentation subsequently led to large-scale mortality. Thus, restoration approaches that can avoid areas with high sedimentation or that can ameliorate its effects (e.g. greater vertical relief of substrate, alternative substrates) could enhance restoration success in this system. However, inferences from the predation tile experiment suggest that ameliorating the effects of sedimentation may enhance predation. Thus, successful restoration in this system may also require finding sites with less predation, or efforts to control predation such as planting larger remote-set oysters on the reefs to reestablish viable populations.

While we were not able to identify a definitive set of optimal conditions for successful restoration in the studied system, the results of this study provide regionally specific insights into the effect of biotic and abiotic gradients on oyster settlement, survival and growth. To judiciously allocate limited restoration funding, restoration guidance frameworks based on insights from rigorous monitoring of restoration projects are critical (Baggett et al. 2015, Walles et al. 2016). The comprehensiveness of these frameworks and their regional transferability will inevitably be dictated by the availability of studies that quantify the effect of biophysical gradients on whether restoration efforts recover lost ecosystem services.

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