FEATURE ARTICLE

Reef height drives threshold dynamics of restored oyster reefs

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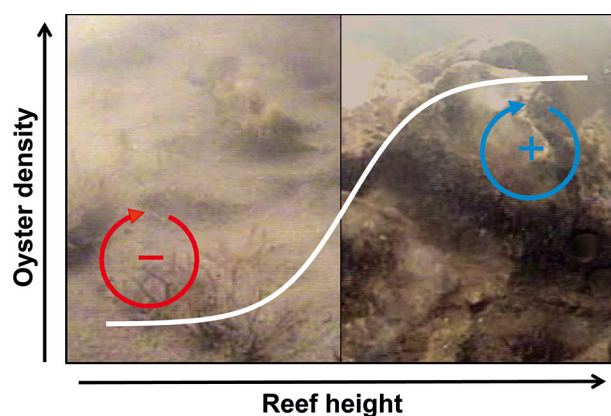
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ABSTRACT: Nonlinear threshold responses to biotic or abiotic forcing may produce multiple population trajectories dependent upon initial conditions, which can reinforce population recovery or drive local extinction, yet experimental tests of this phenomenon are lacking in marine ecosystems. In field experiments at 4 sites in 2 tributaries of lower Chesapeake Bay, we examined demographic responses (density and survival) of eastern oyster *Crassostrea virginica* populations to reef height and associated gradients in sediment deposition and habitat complexity. After 2 yr, oyster reefs exhibited diverging trajectories toward either degradation or persistence, dependent upon initial reef height. Reefs higher than 0.3 m supported greater oyster density, survival, and reef complexity, whereas sediment deposition was reduced. Reefs lower than 0.3 m experienced heavy sediment deposition and were eventually buried. These observations (1) provide experimental evidence for threshold dynamics in marine species, (2) suggest that the collapse of oyster populations was largely due to anthropogenic habitat degradation that eliminated positive feedbacks and which may have created an alternative reef trajectory towards local extinction, and (3) indicate an avenue by which oyster restoration is achievable.

KEY WORDS: *Crassostrea virginica* · Reef height · Sedimentation · Thresholds · Alternative stable states · Oyster reef · Restoration

Feedback mechanisms driven by reef height result in threshold responses of oyster populations leading to diverging reef trajectories toward degradation or persistence.

Photos: Allison M. Colden

INTRODUCTION

Native oyster species have been decimated globally due to overfishing, eutrophication, disease, and habitat degradation (Jackson et al. 2001, Kirby 2004, Lotze et al. 2006, Beck et al. 2011, Zu Ermgassen et al. 2012). Concern over these declines and losses of attendant oyster ecosystem services, such as nutrient cycling, water filtration and habitat structure (Grabowski & Peterson 2007), have spurred efforts to restore oyster populations globally (Airoldi & Beck 2007), but these efforts have seen limited success (Airoldi & Beck 2007, Beck et al. 2011, Kennedy et al. 2011, Zu Ermgassen et al. 2012).

Many oyster species are considered ecosystem engineers, forming large biogenic reefs that provide habitat for oysters and other organisms and structure the estuarine landscape (Dame 1996, Gutierrez et al. 2003). While this bioengineering function provides habitat heterogeneity and promotes biodiversity (Luckenbach et al. 2005), it also renders species less resilient to intensive harvesting and severe habitat degradation (Herman et al. 1999, Scheffer et al. 2001, Dame et al. 2002, Wilberg et al. 2013). The collapse of oyster populations around the world has often in-

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volved phase shifts from a productive state that supports self-sustaining populations and biodiversity to one that is severely degraded (Zu Ermgassen et al. 2013). For bivalve reefs, these conditions likely represent alternative stable states, which are invoked by positive feedbacks and exhibit complex, nonlinear dynamics (Herman et al. 1999, Dame et al. 2002). It has been hypothesized that a major obstacle preventing ecosystem recovery following perturbation stems from the elimination of positive feedbacks that maintain productive ecosystem states (Folke et al. 2004, Donadi et al. 2014).

Recent studies have identified oyster reef geometry, particularly height above the seabed, as an important factor driving restoration success, presumably due to positive feedbacks between reef structure, hydrodynamics and resulting population dynamics (Lenihan 1999, Powers et al. 2009, Schulte et al. 2009, Lipcius et al. 2015, Theuerkauf & Lipcius 2016). Lenihan (1999) determined that oyster growth and survival was highest on crests of reefs >1.0 m while sedimentation and mortality was highest at the base of reefs and on short reefs (0.1 m). These differences were driven mainly by flow speed, which varied with reef height and influenced sedimentation patterns. Schulte et al. (2009) and Lipcius et al. (2015) determined that high-relief reefs (0.25 to 0.45 m) had higher oyster abundances and tended to persist while low-relief reefs (0.08 to 0.12 m) had lower abundances and were variable in their success. Similarly, Powers et al. (2009) determined that sedimentation was a major factor influencing the success of restored oyster reefs and that a minimum of 0.2 m relief was required for restoration success. Along the South Atlantic Bight, higher reef relief was associated with faster flow speeds and higher oyster recruitment and biomass (Byers et al. 2015). For *Ostrea lurida*, shell beds constructed at 0.12 m resulted in greater recruitment, higher adult density, and lower sedimentation than 0.04 m beds (Zacherl et al. 2015). These studies suggest that high-relief reefs tend to produce self-sustaining, productive reefs while low-relief reefs perform poorly or degrade to extinction, but the range of heights used is too coarse to identify the point at which the trajectory changes from persistence to degradation.

This dichotomy of restoration outcomes has been repeatedly observed across geographic locations, time scales, and even different oyster species, suggesting there is a common mechanism underlying oyster population responses to reef geometry. Modeling studies suggest that these outcomes represent 2 alternative stable states of oyster reef ecosystems (Jordan-Cooley et al. 2011, Wilberg et al. 2013, Housego & Rosman 2016) that result from biophysical feedbacks responding to initial reef height. Elevation of the reef above the seafloor restricts the height of the water column as it passes over the reef, resulting in faster flow rates relative to non-constricted flow (Lenihan 1999). If flow rates are sufficient to promote sediment erosion from the reef and break down feeding-inducing concentration gradients, this could result in increased recruitment, growth, and survival of the oyster population (Lenihan 1999, Byers et al. 2015). Jordan-Cooley et al. (2011) suggest a bifurcation point for reef populations above which reefs and live oyster populations increased to a non-zero equilibrium and persisted over time and below which reefs were overwhelmed by sediment and degraded to extinction in less than 20 yr. Other models demonstrate similar dynamics to those described by Jordan-Cooley et al. (2011) in response to different initial reef height conditions (Wilberg et al. 2013, Housego & Rosman 2016).

Despite repeated observations of these distinct oyster reef trajectories and evidence for threshold dynamics in other bivalve species (van de Koppel et al. 2005, Walles et al. 2015b), identification of a threshold at which these trajectories diverge and the mechanisms that drive them have not been quantified. We designed a large-scale field experiment to (1) determine if the threshold of initial reef height suggested in previous studies is realized in the field under identical environmental conditions, and (2) identify the mechanism(s) by which height influences reef trajectory. The identification of threshold responses to reef height would provide insights on the systemic collapse of oyster ecosystems worldwide and provide context for reef ecosystems that have failed to recover despite restoration efforts (Suding et al. 2004, Kennedy et al. 2011). It would also provide a means by which restoration managers can better understand the mechanistic drivers of restoration and utilize these dynamics to optimize limited resources.

MATERIALS AND METHODS

Field experiment

In July 2009, we constructed 24 subtidal experimental oyster reefs across 4 sites in the Great Wicomico (GWR1, GWR2) and Lynnhaven (LR1, LR2) Rivers, 2 sub-estuaries of Chesapeake Bay in Virginia, USA. Study sites were chosen based on standard restoration site criteria: water depth <3 m, sand

to muddy-sand bottom, and close proximity to oyster broodstock (Woods et al. 2004, Theuerkauf & Lipcius 2016). Sites within rivers represented a range of energetic conditions, as characterized by their geographic location, fetch, and sediment type, with one high-energy (GWR1, LR2) and one low-energy (GWR2, LR1) site in each river.

Reefs were constructed of eastern oyster *Crassostrea virginica* shell with a 0.03 m base layer of crushed surf clam *Spisula solidissima* shell at 6 experimental reef heights (0.05, 0.1, 0.2, 0.3, 0.4, 0.5 m above the bed; Fig. 1). This range of reef heights encompasses those typically used in oyster restoration or repletion activities in Chesapeake Bay (0.05 to 0.1 m; Wilberg et al. 2013) and heights shown to produce 'successful' reefs (Schulte et al. 2009, Lipcius et al. 2015). Reefs were circular (1.3 m diameter) and plateau-shaped to maximize the area of intended height (Fig. 1). Placement of reef height treatments was randomized within each site, and reefs were oriented parallel to the adjacent shoreline with approximately 15 m between reefs. The size and placement of reefs were designed to minimize hydrodynamic interactions between reefs while maintaining constant hydrographic conditions and larval subsidy within the study area. Because the influence of a reef on physical processes scales with reef length (Walles et al. 2015a, Colden et al. 2016), larger reefs would have required a greater distance between reefs to avoid interactions, making it difficult to maintain consistent depth and hydrographic conditions across the study area, a key component when investigating the potential for alternative stable states (Peterson 1984). Qualitative video monitoring was conducted shortly (2 mo) after construction using a remotely operated vehicle to assess the condition of reef habitat.
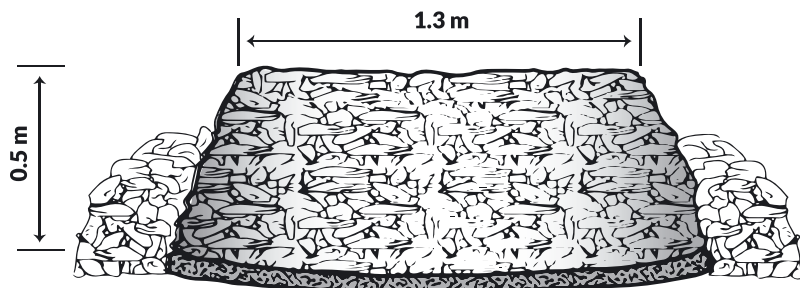

Fig. 1. Experimental reef design for investigation of threshold dynamics of restored oyster reefs in tributaries of lower Chesapeake Bay. Darker shading indicates a 0.03 m base layer of crushed surf clam *Spisula solidissima* shell. The remainder of the reef was constructed using eastern oyster *Crassostrea virginica* shell, including a buffer of oyster shell at the periphery of each reef to prevent shell scattering. The highest reef height treatment (0.5 m) is depicted; heights of other treatments were 0.05, 0.1, 0.2, 0.3, and 0.4 m

To evaluate the proposed mechanisms controlling reef persistence, we measured sediment deposition rate and rugosity, a measure of surface complexity. Sediment deposition rates were measured using sediment traps deployed on the reefs for 7 d in fall 2009. Net sediment deposition varies due to seasonal inputs, rainfall, storm frequency, and other factors. Because particle flux is high (Dame 1987, Lenihan 1999) and erodibility is low (Friedrichs et al. 2008), fall deposition rates are expected to represent maximal seasonal deposition. Cylindrical sediment traps constructed from PVC pipe (25 × 2.1 cm, inner diameter 1.6 cm, aspect ratio 11.9; White 1990) were embedded within the reef matrix such that the opening of the sediment trap was flush with the reef surface. Because of the aspect ratio of the traps and the energetic conditions of our study sites, we suspect there was very little resuspension and subsequent erosion of sediment from the traps (White 1990); therefore, sedimentation on experimental reefs is likely to be less than that observed in the traps.

At retrieval, sediment traps were capped in place, removed from the reef, and transported to the lab on ice where they were processed immediately. Sediment was vacuum filtered on pre-weighed glass fiber filters (Whatman GF/F, 47 mm diameter, 0.7 µm pore size) then dried for 24 h at 70°C and weighed to the nearest 0.001 g. Sediment volumes were converted to deposition rates by scaling the trap opening area (2.0 cm^2) to 1 m^2 and dividing the total sediment dry volume by the deployment interval (7 d).

Rugosity, an index of surface complexity, is determined by small-scale heterogeneity in the reef surface produced by interstices in the shell substrate and settlement and growth of oysters. Rugosity was measured using the chain and tape method (Frost et al. 2005), in which a fine link chain is laid over the surface of the reef within the reef margin, allowing the chain to conform to the crevices of the reef. This length is divided by the reef's linear length to produce an index of surface complexity. Larger values indicate more structurally complex surfaces; a value of 1 indicates a flat surface. Surface roughness influences mass flux (Reidenbach et al. 2010), larval recruitment (Soniat et al. 2004), and trophic interactions (Grabowski et al. 2008). Heavy sedimentation reduces surface complexity; thus rugosity provides an additional measure of the impact of sediment on reefs. Four

replicate measurements were made on each reef parallel to the adjacent shoreline along the reef diameter. These values were averaged to determine the reef rugosity index.

Oyster density and survival were measured 8 and 24 mo following reef construction. At each sampling interval, a 1.69 m² quadrat subdivided into 9 equal quadrants was placed on the reef and 2 quadrants were chosen at random for sampling. Within selected areas, all oyster shell and associated epibenthic organisms were excavated down to 0.15 m (Bartol et al. 1999). For reefs with <0.15 m relief, all shell material was excavated. For reefs that were buried at the time of sampling, sediment was removed and the reef was excavated down to 0.15 m or until no shell material was present. To maintain reef height, the excavated material was replaced with clean oyster shell. Quadrants that were sampled at 8 mo were excluded from resampling at 24 mo to avoid confounding effects of substrate age. At each sampling interval, live and dead oysters were counted and left valves were measured to the nearest 0.1 mm shell height.

Statistical analysis

To identify possible threshold dynamics between initial reef height and oyster density, sediment deposition, and rugosity, we used nonlinear least squares regression to determine the shape of the functional relationship between variables by fitting a suite of candidate base models (Table 1). The base models included a linear function to rule out a lack of nonlinearity in the response (Hsieh et al. 2005), a symmetrical threshold function (logistic), an asymmetrical threshold function (Gompertz), and a nonlinear monotonic function (power function). Akaike's Information Criterion corrected for small sample size (AICc) was

Table 1. Threshold dynamics of restored oyster reefs in tributaries of lower Chesapeake Bay: candidate base models for nonlinear regression analysis of the relation between initial reef height and sedimentation rate, rugosity, and oyster density. Oyster survival was analyzed by logistic regression only as survival was expressed as the proportion of live oysters and was bounded from 0 to 1

Model	Function
Linear	$y = ax + b$
Logistic	$\dfrac{c}{1 + e^{-a(x-b)}}$
Gompertz	$ae^{-e^{-b(x-c)}}$
Power	$y = ax^b$

used to compare base models to determine the function that best described the form of the relationship between reef height and the response variable (oyster density, sedimentation rate, or rugosity) (Anderson 2008). Effect sizes and model fit for models with AICc weights greater than 0.1 were examined to determine the best-fitting model, which was retained for covariate analysis. (Anderson 2008).

For each response variable, covariates were added to the base model to quantify the influence of site-specific variation on the form of the functional relationship (Kimura 2008). For the selected base model, a site covariate was added to the coefficient (power) or maximum value (logistic, Gompertz) and/or the shape parameter to determine the nature of the site-specific response (Kimura 2008). Significance of covariates was determined by comparing the AICc value and effect sizes of the covariate model with that of the base model. Model validity was confirmed by likelihood ratio tests comparing each covariate candidate model to the null (intercept-only) model.

Because oyster survival was measured as a proportion of live oysters, logistic regression was used to determine the effect of reef height (Warton & Hui 2011). A covariate model including site-specific variation in oyster survival was fit to the logistic function with AICc model comparisons as previously described.

RESULTS

Reef condition

Qualitative video sampling of experimental reefs indicated a divergence in reef condition almost immediately following construction (within 2 mo). Reef conditions on 0.05 to 0.2 m reefs were typified by sedimentation and shell burial, particularly around the reef margins, which was especially heavy at LR2, the high-energy site in the Lynnhaven River (Fig. 2a). Reefs ≥0.3m exhibited emergent shell, evidence of successful oyster recruitment, and lower levels of sedimentation (Fig. 2b). At LR2, it appeared that bedload activation and sediment transport were high (discussed below), and all reefs at this site were buried before the conclusion of the study at 24 mo. At all other locations, taller reefs (≥0.3 m) remained emergent throughout the duration of the experiment, while some low-relief reefs (<0.3 m) were buried at GWR1 and GWR2. At LR1, the low-energy site in the Lynnhaven River, all reefs remained emergent throughout the duration of the study, though burial of shell at the reef margins was evident.
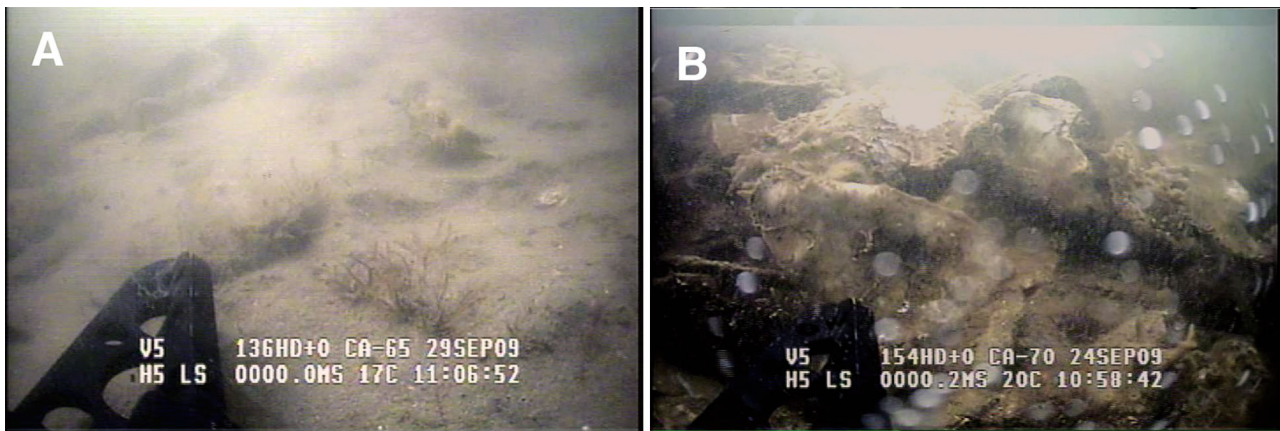
Fig. 2. Remotely operated vehicle (ROV) images of typical (A) low- and (B) high-relief restored oyster reefs in 2 tributaries of lower Chesapeake Bay (Great Wicomico River [GWR]; Lynnhaven River [LR]), 2 mo after construction: (A) a 0.1 m reef at site LR2; (B) a 0.5 m reef at site GWR1. The ROV's sampling arm is visible in the lower left of each photograph

Sediment deposition and reef rugosity

Sediment deposition rate declined exponentially with increasing reef height (Fig. 3, Tables 2 & 3), with the exception of one site (LR1). At LR1, deposition rates were extremely low (0.017 ± 0.001 g dry weight [DW] d^{-1}, mean $\pm$ SE) and regression parameters were not significantly different from zero ($p > 0.05$). The LR2 site represented the opposite extreme in

sediment deposition, exhibiting the highest deposition rates (3.42 ± 1.31 g DW d^{-1}), which were 2 orders of magnitude greater than other sites. The remaining 2 sites in the Great Wicomico River, GWR1 and GWR2, experienced intermediate sediment deposition (0.07 ± 0.02 and 0.02 ± 0.002 g DW d^{-1}, respectively) relative to LR sites. At GWR1 and GWR2, the 2 lowest-relief reefs (0.05, 0.1 m) were nearly buried (>90% burial) by the conclusion of the experiment
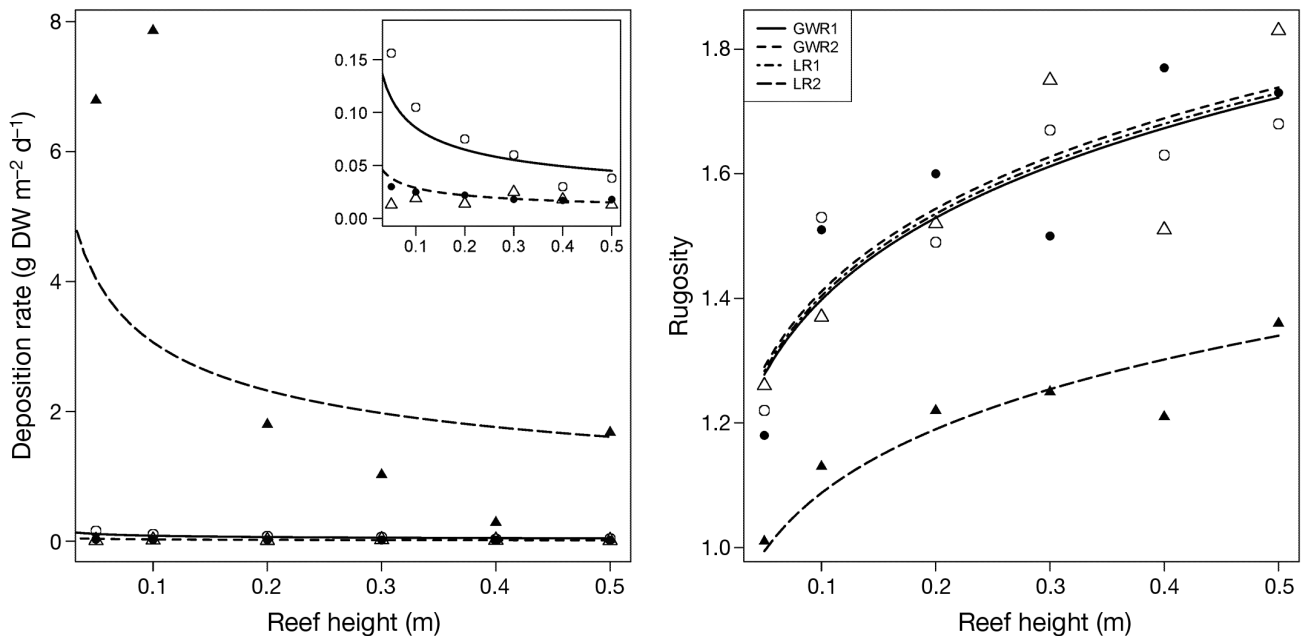

Fig. 3. Physical responses to reef height on restored oyster reefs at 4 experimental sites in 2 tributaries of lower Chesapeake Bay (Great Wicomico River [GWR]; Lynnhaven River [LR]): (O) GWR1; (●) GWR2; (△) LR1; (▲) LR2. Left: sediment deposition rate; right: rugosity. The inset in the left panel shows sediment deposition rates at sites GWR1, GWR2, and LR2 with an expanded y-axis scale. Curves show the results of regression analysis. No regression is shown for LR1 for sediment deposition because regression parameters were not significantly different from zero due to extremely low levels of deposition

Table 2. Results of model comparison using Akaike's Information Criterion corrected for small sample size (AICc) for base models of the relation between reef height and sediment deposition and rugosity. The best-fit models chosen for covariate analysis are indicated in **bold**. w is the weighted probability that the model selected is the best of the candidate model set

Model	AICc	ΔAICc	w
Sediment deposition			
Power	**68.88**	**0.000**	**0.960**
Linear	75.23	6.352	0.040
Logistic	101.4	32.51	<0.001
Gompertz		Did not converge	
Rugosity			
Power	**−10.81**	**0.000**	**0.492**
Linear	−8.867	1.942	0.186
Gompertz	−8.616	2.193	0.164
Logistic	−8.541	2.268	0.158

while taller reefs (>0.2 m) persisted. Covariate analysis indicated that the regression with shape parameters varying across study sites was the best model fit (Table 3), such that the rate at which deposition rate decreased across reef heights varied between sites, likely due to the availability of suspended sediments at various sites.

Rugosity responded in the inverse to sediment deposition (Fig. 3, Tables 2 & 3). The functional relationship between reef height and rugosity was best described by a power function with shape parameters varying across sites. Rugosity was much lower at LR2, the site that experienced sediment deposition rates that were 2 orders of magnitude greater than the other sites. This was also the only location at which one of the reefs (0.05 m) had a rugosity score of

Table 3. AICc model comparison results for site covariate models of sediment deposition rate and rugosity with the coefficient (*a*), shape parameter (*b*), or both, modified by the site covariate. p-values are presented for likelihood ratio tests of the given model compared to the null (intercept-only) model. The AICc best-fit model is indicated in **bold**. w: weighted probability that the model selected is the best of the candidate model set

Base model	Site covariate	AICc	ΔAICc	w	$p(\chi^2)$
Sediment deposition					
$y = ax^b$	**b**	**−49.37**	**0.000**	**1.000**	**<0.001**
	None	68.88	118.2	<0.001	<0.001
	a	9.116	58.49	<0.001	<0.001
	a and b		Did not converge		
Rugosity					
$y = ax^b$	**b**	**−42.15**	**0.000**	**0.918**	**<0.001**
	a and b	−37.31	4.840	0.081	<0.001
	a	−26.54	15.61	<0.001	<0.001
	None	−10.81	31.34	<0.001	<0.001

1, indicating a completely homogeneous surface. At the remaining sites, rugosity increased with reef height to a maximum of 1.83. Mean rugosity was significantly different (ANOVA, p = 0.001) for reefs below (1.33 ± 0.05) and above (1.57 ± 0.06) 0.2 m in reef height. Like sediment deposition rates, the shape of the relationship between reef height and rugosity varied across sites (Table 3), which was again likely due to the differences in sediment availability between sites.

Oyster density and survival

At all sites in both sampling periods, we observed nonlinear responses of oyster density with respect to reef height (Fig. 4, Tables 4 & 5). The functional relationship between reef height and oyster density was best characterized as logistic, indicating a change point in the form of the function across reef heights at 0.27 ± 0.03 m (mean ± SE) and 0.33 ± 0.07 m in the 8 and 24 mo sampling periods, respectively. The asymptote of the logistic function varied across sites at both the 8 and 24 mo sampling periods, but shape parameters did not differ between sites, suggesting that although the maximum number of oysters differed across sites the functional relationship and estimated density threshold did not vary across sites (Table 5). Variation in maximum oyster density was likely due to differences in larval availability across sites that was reflected in oyster recruitment. Oyster densities on reefs at or above the average estimated threshold (0.3 m) were 3.5 times higher (499.3 ± 56.2 m^2) than on reefs below the estimated threshold (0.05 to 0.2 m, 140.6 ± 18.2 m^2), with a significant difference in average density between reefs above and below the threshold (ANOVA, p < 0.001). Although there was notable variation in oyster density between sites at 8 mo, oyster density response to reef height was much less variable across sites after 24 mo (Fig. 4).

Oyster survival relative to initial reef height varied widely across study sites during the first sampling interval (Fig. 4, Tables 4 & 5). Survival increased with reef height at the LR2 site after 8 mo, with a threshold in survival at approximately 0.4 m (Fig. 4, Table 4); however, the remaining 3 sites did not demonstrate significant effects of reef height on survival after
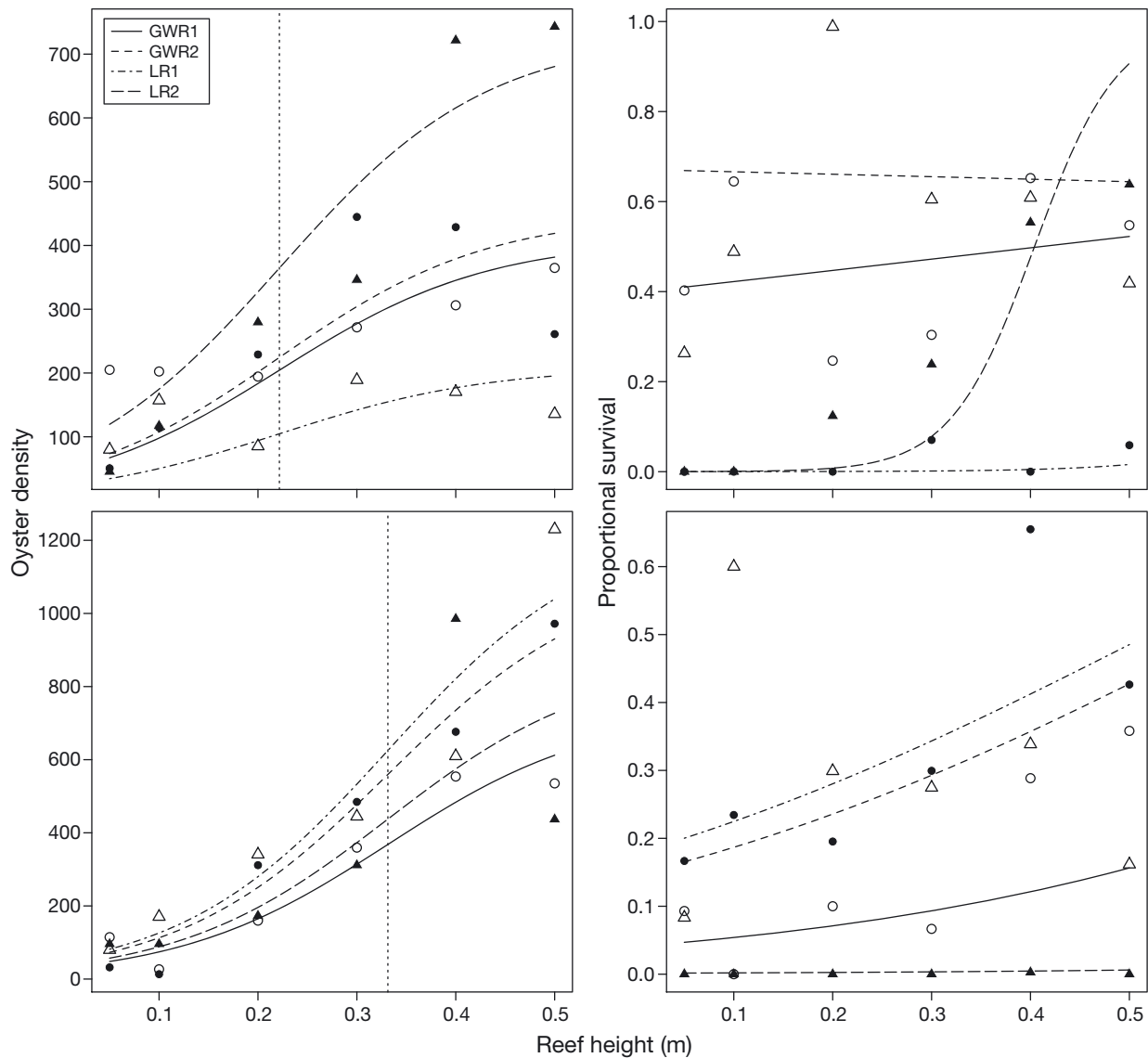
Fig. 4. Oyster density and survival as a function of reef height on restored oyster reefs at 4 experimental sites in 2 tributaries of lower Chesapeake Bay: (O) GWR1; (●) GWR2; (△) LR1; (▲) LR2. Nonlinear response of oyster density (left panels) and survival (right panels) to initial reef height at 8 mo (top) and 24 mo (bottom) post-construction. Curves show the results of regression analysis. Vertical dotted lines indicate the threshold in initial reef height estimated by the inflection point of the curve

8 mo (p > 0.05; Fig. 4) At 24 mo, survival increased monotonically with reef height at all sites except LR2 (Fig. 4, Table 4), where all reefs experienced complete burial and total mortality prior to the 24 mo sampling period. Covariate analysis indicated that both the shape of the function and maximum survival varied across sites (Table 5), which is reflected in the variation of the functional relationship across sites (Fig. 4).

To visualize the trajectory of reefs above and below the average estimated threshold, oyster density for each reef was normalized by study location

and tracked over time (8 vs. 24 mo; Fig. 5). LR2 was excluded from this analysis since reefs at that location did not experience a second recruitment event due to burial. Although density on reefs above and below the threshold overlapped 8 mo post-construction, over time densities converged within groups and diverged between groups, such that average densities of the 2 groups were clearly separated in the second year. The majority (86%) of high-relief reefs (>0.3 m) increased in density over time, while 42% of low-relief reefs decreased in density (Fig. 5).

DISCUSSION

Nonlinear threshold responses of oyster reefs

After 24 mo, experimental reefs demonstrated 2 distinct trajectories, persistence or degradation, with the trajectory associated with local sediment deposition rates and initial reef height. These conditions were consistent across temporal and spatial scales, indicating that there is a common mechanism underlying the persistence or degradation of reefs based on their initial height.

Table 4. AICc model comparison results for base models of the relation between reef height and oyster density. The best-fit model chosen for covariate analysis is indicated in **bold**. w: weighted probability that the model selected is the best of the candidate model set

Month sampled	Model	AICc	ΔAICc	w
Density				
8	**Logistic**	**312.8**	**1.284**	**0.224**
	Gompertz	312.9	1.428	0.209
	Linear	311.5	0.000	0.426
24	**Logistic**	**315.0**	**0.000**	**0.323**
	Gompertz	315.2	0.203	0.290
	Linear	319.1	4.087	0.042

Table 5. AICc model comparison results for site covariate models of oyster density and survival at 8 and 24 mo sampling intervals with either the shape parameter (a) or asymptote (c) or both modified by the site covariate. b: estimated threshold (inflection point) of the function. p-values are presented for likelihood ratio tests of the given model compared to the null (intercept-only) model. The AICc best-fit model is indicated in **bold**. w: weighted probability that the model selected is the best of the candidate model set

Month sampled	Base model	Model	AICc	ΔAICc	w	$p(\chi^2)$
Density						
8	$\dfrac{c}{1+e^{-a(x-b)}}$	c	**315.0**	1.767	0.237	0.005
		None	312.8	0.000	0.574	0.001
		a	314.5	2.228	0.188	0.006
		a and c	Did not converge			
24	$\dfrac{c}{1+e^{-a(x-b)}}$	c	**315.0**	**0.000**	**0.827**	**0.006**
		a	319.4	4.453	0.089	0.038
		None	319.6	4.569	0.084	0.058
		a and c	Did not converge			
Survival						
8	$\dfrac{c}{1+e^{-a(x-b)}}$	**a and c**	**113.12**	**0.000**	**0.980**	**<0.001**
		c	120.86	7.740	0.020	<0.001
		a	135.48	22.35	<0.001	0.015
		None	138.58	25.48	<0.001	0.072
24	$\dfrac{c}{1+e^{-a(x-b)}}$	**a and c**	**75.16**	**0.000**	**0.715**	**<0.001**
		c	77.01	1.844	0.284	<0.001
		a	93.56	18.39	<0.001	<0.001
		None	112.27	37.10	<0.001	0.305

The persistence of oyster reefs depends on the balance of processes that maintain and grow the reef (recruitment, growth, biodeposition) and those that degrade it (burial, sedimentation, shell degradation). Thus, the persistence of an oyster reef is heavily dependent on the dynamics of the oyster population (Powell & Klinck 2007, Rodriguez et al. 2014, Walles et al. 2015b). In this study, we demonstrated that oyster density exhibits a nonlinear threshold response with respect to initial reef height. The mean threshold value was 0.3 m: Reefs with initial heights ≥0.3 m had higher oyster densities that generally increased over time whereas reefs ≤0.2 m maintained lower oyster densities that tended to decrease over time under a range of sedimentation rates. This threshold value (0.3 m) falls within the range of reef heights (0.25 to 0.45 m) that previously produced 'successful' reefs in Chesapeake Bay (Schulte et al. 2009, Lipcius et al. 2015), and corresponds with previous success metrics (>0.2 m) for projects in North Carolina (Powers et al. 2009) and a 0.3 m 'rule of thumb' for projects in New Hampshire (Grizzle & Ward 2016). Other reef-building *Crassostrea* species, such as *Crassostrea gigas*, also exhibit thresholds in reef persistence at approximately 0.25 m (Walles et al. 2016).

Nonlinear threshold dynamics in oyster density are significant because reef accretion processes, which must outpace degradation for reefs to persist, depend on the demography of the population (Powell & Klinck 2007, Rodriguez et al. 2014, Walles et al. 2015b). Recruitment, growth, and survival generally respond positively to increasing water flow (Byers et al. 2015), up to flow speeds of approximately 7 cm s^{-1} (Lenihan et al. 1996); thus taller reefs experience higher flow rates and consequently support larger oyster populations (Lenihan 1999). Our experimental reefs exhibited a significantly higher (3.5 fold) number of oysters on reefs ≥0.3 m relative to reefs ≤0.2 m. This impacts local population dynamics through reproduction, in which a larger population of oysters is able to produce a greater number of larvae to recruit to the reef (Schulte & Burke 2014), to the extent that reefs are self-recruiting, and through the provision of shell, which provides a suitable settlement surface.
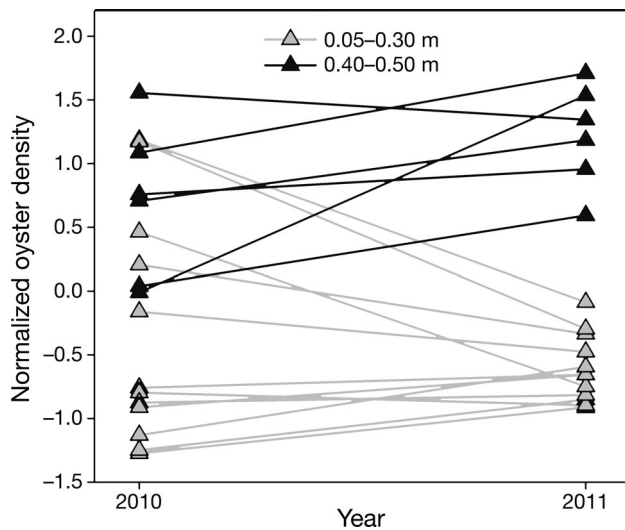
Fig. 5. Trajectories of oyster density on restored oyster reefs at 4 experimental sites in 2 tributaries of lower Chesapeake Bay. Trajectories over 2 yr are shown for reefs (▲) above and (△) below the average estimated reef height threshold (0.3 m). Values for site LR2 are excluded as reefs at that location were buried prior to the second recruitment event

Mortality is also an important component of reef persistence as shell contributes to the reef matrix; however, it must be balanced with recruitment and survival to ensure the population can further contribute to the reef (Powell & Klinck 2007). Unlike oyster density, we did not observe a threshold response of oyster survival to reef height, except at LR2, the site experiencing the highest sediment challenge. At the first sampling interval, LR2 exhibited a threshold in survival at approximately 0.4 m, while other sites showed no clear relationship between survival and reef height. After 2 yr, the site with the highest sediment deposition rate (LR2) experienced 100% mortality, and remaining sites exhibited increasing survival with increasing reef height, but no threshold. Lenihan (1999) showed that reef height explained 29% of the variance in mortality on reefs ranging from 0.1 to 2.0 m in height, with the highest mortality on 0.1 m reefs. Additionally, mortality was higher on the bases of reefs relative to the crest, where reduced sedimentation promoted oyster survival.

Mechanisms and positive feedbacks

The dichotomy of reef trajectories based on initial reef height observed in this study and others (Lenihan 1999, Taylor & Bushek 2008, Powers et al. 2009, Schulte et al. 2009) across a wide range of locations and time scales suggests a common mechanism is driv-

ing dynamics of *Crassostrea virginica* reefs throughout its geographic range. Population models suggest that sediment deposition mediated by initial reef height is capable of producing alternative stable equilibria similar to reef outcomes observed in the field (Jordan-Cooley et al. 2011, Wilberg et al. 2013, Housego & Rosman 2016). In these models, a stable, non-zero equilibrium is achieved when live oyster and shell volume growth outpaces sediment deposition, which varies with reef height and reaches a maximum at the seafloor (Jordan-Cooley et al. 2011, Housego & Rosman 2016). It has been suggested that sediment deposition is a result, not a cause, of oyster reef decline (Powell & Klinck 2007). In contrast, this study demonstrates that the physical structure of the reef alone can directly impact sediment deposition rates with resulting effects on oyster population size.

Sediment deposition decreased monotonically with reef height at 3 (LR2, GWR1, GWR2) out of 4 study sites. At LR1, deposition rates were extremely low and did not show a significant relationship to reef height. This decline in sediment deposition with reef height mirrors the processes included in the population models and previous field observations (Lenihan 1999), which indicated sediment deposition was greatest on low-relief reefs and at the bases of reefs relative to the crest.

Sedimentation impacts oyster populations directly through burial that smothers oysters, causing mass mortality (Norris 1953, Dunnington 1968, Miller et al. 2002, Twichell et al. 2010), and indirectly through partial burial that degrades habitat quality and reef-building processes (Colden & Lipcius 2015). At the study site with the highest sediment deposition rates (LR2), indications of heavy sedimentation were evident 2 mo following construction, and full burial of reefs occurred between 8 and 24 mo post-construction. This is consistent with previous field observations in which low-relief reefs were buried after 16 mo (Lenihan 1999). Sediment covering the reefs at this location (LR2) was similar in composition to the sediment in the surrounding area (A. Colden pers. obs.); so it is likely that burial at this location was due to activation and transport of bedload sediments that buried nearby reefs, similar to burial events described in Taylor & Bushek (2008). In this high-energy location, this range of reef heights was insufficient to overcome shifting sediments and high rates of deposition. Despite the burial of reefs at LR2, early recruitment (prior to reef burial) exhibited a threshold response to initial reef height similar to other study locations. At sites with intermediate deposition rates (GWR1, GWR2), results mirrored previous studies (Schulte et

al. 2009), in which low-relief reefs experienced heavy sedimentation and supported significantly fewer oysters than high-relief reefs. Some of the lowest relief reefs at these sites were completely buried by the conclusion of the experiment, whereas reefs ≥0.3 m persisted. In areas where sediment buried a portion of or the entire reef surface, deposition was concentrated at the reef margin, which corresponds to patterns of reef burial for circular 'patch' reefs (Colden et al. 2016). In low deposition environments, like that of LR1, sedimentation was not significantly influenced by reef height because low deposition rates were insufficient to produce quantifiable differences across reef heights. All reefs at this location were present at the end of the 2 yr study, though some burial at the reef margin was also present. This is similar to conditions described for other erosive estuaries where reef heights of approximately 0.25 m are sufficient to ensure reef persistence (Walles et al. 2016). Along the South Atlantic Bight, reefs < 0.25 m often persist despite high sedimentation rates because of high tidal energy and flow speeds that promote oyster growth and erode sediment from the reef surface (Byers et al. 2015).

Margiotta et al. (2016) demonstrated that rugosity scales with shell volume, as it did in this study, with reef height directly proportional to shell volume. Rugosity values reported here were within the range of values previously reported for *C. virginica* reefs (Harwell et al. 2010, Margiotta et al. 2016), and values for sites with low sediment deposition (GWR2, LR1) exceeded published rugosity values. This indicates that sediment deposition had a demonstrable effect on reef heterogeneity, as the site with highest deposition (LR2) exhibited much lower rugosity values than the other 3 sites, even though rugosity increased with shell volume across all sites.

Rugosity is an important element of the reef-sediment feedback loop because it impacts biological and physical processes on the reef influencing reef productivity and accretion. At the reef scale, surface roughness enhances turbulence above the reef surface, magnifying particle flux (Reidenbach et al. 2010, Whitman & Reidenbach 2012) and augmenting sediment erosion from the reef surface (Colden et al. 2016). At the millimeter to centimeter scale, reef heterogeneity creates complex interstices, providing larger surface area and low-flow refugia within the reef matrix for oysters to settle (Soniat et al. 2004, Whitman & Reidenbach 2012). Habitat complexity can also promote survival by mediating predator interactions that ultimately benefit juvenile oysters (Grabowski et al. 2008) and other reef resident species (Humphries et al. 2011). While it is impossible to fully disentangle the impacts of rugosity and reef height on reef persistence, it is clear that these 2 aspects of reef geometry play a critical role in determining the fate of oyster reefs by mediating important biophysical feedbacks leading to stability and persistence or degradation and reef loss.

Implications for oyster restoration

The threshold dynamics observed in this study are a likely explanation for both the initial loss of reef habitats along the Atlantic coast (Scheffer et al. 2001, Kirby 2004) and for the failure of many repletion and restoration efforts that utilized low-relief reefs (Schulte et al. 2009, Kennedy et al. 2011, Wilberg et al. 2013). Destructive harvesting techniques like dredging and hydraulic tonging reduce the height of reefs by disaggregating the reef structure and removing accreted oyster shells along with live oysters (Lenihan & Peterson 1998). This study demonstrates that the reduction of reef height below a critical threshold will cause the reef to move from a persistent to a degrading trajectory, even in the absence of harvest (Scheffer et al. 2001), unless interventions to rebuild and maintain reef structures above the threshold are carried out. Metabolic stress from sedimentation exacerbates the effects of reef degradation, further contributing to reef decline (Lenihan et al. 1999) and resulting in a trajectory toward reef extinction.

This study also demonstrates that a single aspect of reef geometry, reef height, can be sufficient to produce divergent population trajectories over time and that the scale of reef height over which these trajectories diverge is relatively small (approximately 0.1 m). This is beneficial for restoration practitioners as height is one aspect of reef construction that is easily manipulated, which can be utilized to avoid overbuilding and conserve resources. Alternatively, it demonstrates that restoration reefs that are constructed below the necessary threshold will often produce conditions incompatible with long-term persistence. It also indicates that restoration reefs should be off-limits to harvest unless managers are able to ensure reefs maintain a stable or positive shell budget at or above the reef height threshold under harvest conditions (Powell & Klinck 2007, Wilberg et al. 2013).

Potential for alternative states

The experimental demonstration of alternative stable states has proven difficult in marine systems and

the conditions necessary to identify alternative states remain equivocal (Petraitis & Dudgeon 2004, Hsieh et al. 2005). Nevertheless, there are several criteria that strongly suggest the existence of alternative states for oyster reefs under anthropogenic influence. If different initial conditions produce different final states under the same environmental conditions or within the same habitat, there is strong evidence for alternative states (Scheffer & Carpenter 2003, Petraitis & Dudgeon 2004). This study is unique as it provides direct experimental manipulation of initial reef conditions under the same environmental conditions within study sites, replicated across several sites and geographic locations. This design provides strong empirical evidence for the existence of 2 alternative states for oyster populations, an extinction or low-density state characterized by heavy sedimentation and reef burial or degradation, and a high-density state characterized by low sedimentation, high oyster density, and persistence. Though the experimental reefs used in this study were relatively small, the end-points observed here have been demonstrated repeatedly for large-scale (hundreds to thousands of square meters) restoration projects across multiple geographic locations, suggesting that these reefs were able to induce conditions similar to those observed on larger reefs (Lenihan 1999, Taylor & Bushek 2008, Powers et al. 2009, Schulte et al. 2009, Lipcius et al. 2015). This field study validates the mechanisms theorized in several previous modeling exercises (Jordan-Cooley et al. 2011, Wilberg et al. 2013), and demonstrates that these models have practical value in their ability to predict long-term outcomes of restoration. It also underscores the need to parameterize such models with a realistic range of sediment deposition values for the intended restoration area, as local sedimentation rate can dramatically influence outcomes.

Understanding the nonlinear response of restored systems to different initial conditions is critical for the success of ecological restoration. More importantly, understanding the mechanistic drivers can provide insights into the dramatic shifts observed in natural systems, leading to more effective restoration and management.

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