
Settlement and Survival of the Oyster *Crassostrea virginica* on Created Oyster Reef Habitats in Chesapeake Bay

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Abstract

Efforts to restore the Eastern oyster (*Crassostrea virginica*) reef habitats in Chesapeake Bay typically begin with the placement of hard substrata to form three-dimensional mounds on the seabed to serve as a base for oyster recruitment and growth. A shortage of oyster shell for creating large-scale reefs has led to widespread use of other materials such as Surf clamshell (*Spisula solidissima*), as a substitute for oyster shell. Oyster recruitment, survival, and growth were monitored on intertidal reefs constructed from oyster and Surf clamshell near Fisherman's Island, Virginia, U.S.A. and on a subtidal Surf clamshell reef in York River, Virginia, U.S.A. At the intertidal reefs, oyster larvae settlement occurred at similar levels on both substrate types throughout the monitoring period but higher levels of post-settlement mortality occurred on clamshell reefs. The oyster shell reef supported greater oyster

growth and survival and offered the highest degree of structural complexity. On the subtidal clamshell reef, the quality of the substrate varied with reef elevation. Large shell fragments and intact valves were scattered around the reef base, whereas small, tightly packed shell fragments paved the crest and flank of the reef mound. Oysters were more abundant and larger at the base of this reef and less abundant and smaller on the reef crest. The availability of interstitial space and appropriate settlement surfaces is hypothesized to account for the observed differences in oyster abundance across the reef systems. Patterns observed emphasize the importance of appropriate substrate selection for restoration activities to enhance natural recovery where an underlying habitat structure is destroyed.

Key words: *Crassostrea virginica*, habitat complexity, oyster reefs.

Introduction

Oyster reefs serve an ecologically important role by providing the predominant natural hard substrate in the characteristically sedimentary environment of the middle Atlantic coastal plain. The three-dimensional structure of oyster reef habitat created by eastern oysters (*Crassostrea virginica*) increases the amount of surface area for attachment and crevices for refuge of newly settled oysters as well as numerous small invertebrates and fishes (Wells 1961; Bahr 1974; Dame 1979; Zimmerman et al. 1989; Coen et al. 1999; Harding & Mann 1999; Posey et al. 1999). In Chesapeake Bay, years of poor resource management of both live oysters and shell, mortality from diseases caused by the protistan parasites, Dermo (*Perkinsus*

marinus) and MSX (*Haplosporidium nelsoni*), and increased sedimentation and environmental degradation have contributed to a dramatic decline in oyster populations and reduced reefs to mere footprints (Hargis & Haven 1988; Hargis 1999). These natural, self-renewing habitats are the focus of many habitat restoration efforts throughout Chesapeake Bay (Kennedy & Sanford 1999; O'Beirn et al. 2000; reviewed by MacKenzie 1996 and Mann 2000).

Efforts to restore oyster reef habitats typically begin with the placement of hard substrata on the seabed to serve as a base for oyster recruitment and growth. Over time, continued settlement and subsequent growth of generations of oysters form a continuous veneer of living oyster reef over the base substrate (Wesson et al. 1999; O'Beirn et al. 2000). Numerous studies have emphasized the importance of vertical relief of these created habitats on oyster growth and survival in altering water flow and sedimentation (Lenihan 1999), and for areas where oysters live intertidally, in elevating the habitat into the intertidal zone (Bartol & Mann 1999; O'Beirn et al. 2000; Voley et al. 2000). Since the early 1990s, reefs in lower Chesapeake Bay have been commonly built as three-dimensional mounds ranging in height from approximately 0.5 to 2 m above the seabed (Wesson et al. 1999; O'Beirn et al. 2000). Although many of these created reefs

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in lower Chesapeake Bay are in the intertidal zone, some are located in deep regions or have settled or eroded and are entirely subtidal. Whether intertidal or subtidal, the structure of these constructed hummocks is intended to offer adequate surface and interstitial heterogeneity for oyster growth and survival and for recruitment and aggregation by other epifaunal species.

The most desirable material used in oyster reef construction is empty *C. virginica* shell secured from local shucking operations or from dredging historic deposits of oyster shell (fossil) reefs. When piled into mounds, oyster shells form an interstitial matrix of voids between the shell pieces. These spaces and the shell surfaces around them provide settlement habitat, refugia from predation, and moderation of physical stress for oysters and associated colonizing fauna (Gutiérrez et al. 2003). Although prior research has shown that oyster larvae prefer to settle on living or recently living shells of conspecifics (Crisp 1967; Veitch & Hidu 1971), shortages of oyster shell have prompted examinations of suitable alternative substrates for reef construction (Mann et al. 1990; Pickering 1996; O'Beirn et al. 2000; Soniat et al. 1991; Soniat & Burton 2005).

One material commonly used as an alternative to oyster shell is Surf clamshell (*Spisula solidissima*) (Wesson et al. 1999). A disadvantage of this material is that during commercial shucking operations and large-scale reef construction, *S. solidissima* shells fracture (either through deliberate crushing to compact the material for landfills or road construction, or unintentionally through repeated handling) into small pieces. During reef construction, these pieces pack tightly together and thus provide limited surface area and limited interstitial space for occupation by oysters and colonizing reef fauna. Overall, interstitial volume afforded by fractured *S. solidissima* shell is significantly less than that provided by oyster shell (O'Beirn et al. 2000). To date, only O'Beirn et al. (2000) have examined the efficacy of the *S. solidissima* shell substrate in large-scale intertidal reef restoration efforts, but similar details have not been quantified for clamshell reefs in subtidal habitats.

The objective of this project was to examine and contrast the oyster recruitment, growth, and survival at different reef elevations on a subtidal *S. solidissima* shell reef at Goodwin Island in lower York River, and intertidal reefs constructed of *C. virginica* shell and *S. solidissima* shell near the mouth of Chesapeake Bay at Fisherman's Island. The results have relevance for the selection and placement of materials and of design strategies for future oyster reef restoration activities.

Study Site and Methods

Site Description

The study area included two created oyster reef sites protected from any commercial harvesting in lower Chesapeake Bay. One site was situated at the mouth of the

York River approximately 1 km north of Goodwin Island (a Chesapeake Bay National Estuarine Research Reserve in Virginia site). An oyster reef base was constructed in spring 1995 of 30,000 bushels (1,057 m³) fractured Surf clam (*Spisula solidissima*) shell on a subtidal sand-flat (Meisner 1995). The reef measured approximately 1,350 m² and extended approximately 1.5 m above the seabed. At low tide, the water over the subtidal reef crest was 1.5 m deep.

The other oyster reef site was located at the Fisherman's Island National Wildlife Refuge near the mouth of Chesapeake Bay at Virginia's eastern shore. During summer 1996, 11 subtidal and intertidal oyster reef habitats were constructed of three substrate materials: *Crassostrea virginica* shell (market size valves, ≥ 7.6 cm shell height), crushed *S. solidissima* shell, and, although not evaluated in this study, pelletized coal ash. The reefs ranged in size from 162 to 364 m² (O'Beirn et al. 2000). Although the Fisherman's Island and Goodwin Island reef systems were characterized by different physical (salinity, tidal range, intertidal vs. subtidal reefs, etc.) and biological (benthic and nektonic community species composition, nutrient regimes, etc.) regimes, separate examinations of these reefs offered an opportunity to evaluate the use of alternative substrates in oyster reef restoration efforts and the efficacy of *S. solidissima* shell reefs under distinctly different conditions.

Oyster Sampling

Sampling of the reef to determine oyster abundance and size at Goodwin Island took place from fall 1999 through summer 2001. Using reference stakes permanently positioned at the reef margins, the surface of the reef was divided into a grid and coordinates were assigned to each cell of the grid. The reef was further subdivided into three depth strata: crest (1.5 m above the seabed), flank (0.8 m above the seabed), and base (0.2 m above the seabed) (Fig. 1A). Within each depth stratum, the coordinates on the reef surface were selected randomly without replacement for each sample (once a cell was sampled, the coordinate of the area was recorded so that sampled areas were excluded from selection at a later date). Within the cell, divers placed a square plastic frame (0.25 × 0.25 m) on the reef surface and all substrate material within the frame was removed by hand to a depth of 10 cm (below this depth, shell and associated sediments were black and indicative of anoxic conditions) and placed in a cloth bag. Samples were transported to the laboratory in ice chests and stored in flow-through seawater tanks until processing. Samples were elutriated within 48 hours of collection over a 500- μ m mesh screen. Six replicate quadrat samples per sampling period were collected from each elevation stratum. All live adult (oysters >30 mm shell height, measured from the hinge to the ventral shell margin), juvenile (≤ 30 mm shell height), and recently dead (with empty, paired, articulated valves with no evidence of interior fouling) oysters were counted and measured.

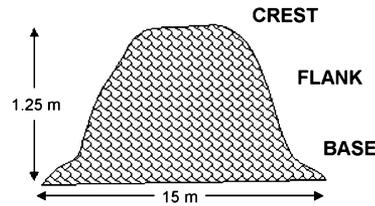
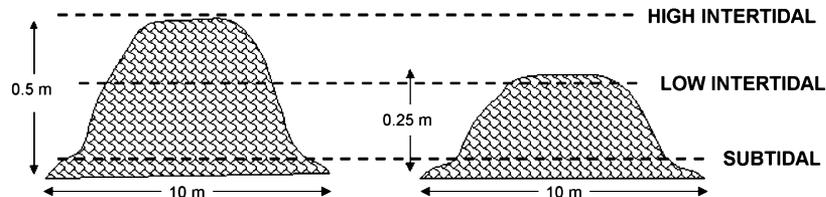
A SUBTIDAL REEF (Goodwin Island)**B INTERTIDAL REEF (Fisherman's Island)**

Figure 1. Sizes and shapes of constructed oyster reefs used in this study. Scale bars are approximate. Reefs are exaggerated vertically for this figure. (A) The subtidal reef at Goodwin Island was constructed of Surf clamshell. Samples were collected from the reef crest, flank, and base. (B) The intertidal reefs at Fisherman's Island (bottom) were constructed of either Surf clam or oyster shell. Regions of the reefs sampled on the intertidal reefs were based on tidal elevation rather than reef morphology. The crests and flanks of different reefs were exposed to different tidal inundation regimes over the course of the study because of settling and erosion of the reefs over time.

Similar methods were used at Fisherman's Island for assessing oyster stocks on the created intertidal reefs (described in detail in O'Beirn et al. 2000). Briefly, in May 1997, 1998, and 1999, three 0.25×0.25 -m quadrats were collected from each of three tidal elevations on two replicate reefs of each substrate type. The elevations were subtidal (0.25 m below mean low water), low intertidal (at mean low water), and high intertidal (0.25 m above mean low water). The crests and flanks of different reefs were exposed to different tidal inundation regimes because of settling and erosion of the reefs over time (in particular, one of the oyster shell reefs) (Fig. 1B). Because the tidal elevation of the reef crests ranged from high to low intertidal, the higher tidal elevations from all reefs were not sampled during the entire study. Therefore, to compare oyster density by reef substrate type, analysis was restricted to the samples collected from the subtidal (reef base) and low intertidal (reef crest or flank, depending on the reef) reef elevations. All live and recently dead (with paired, articulated valves with no interior fouling) oysters were enumerated and measured to the nearest 0.1 mm.

Visual comparisons of the size of Surf clamshell (*S. solidissima*) fragments that made up the Goodwin Islands reef at different elevations were striking and led to a characterization of the reef substrate in July 2000. A subsample of at least 50 shell fragments was randomly selected from each 0.25 m^2 reef quadrat sample and the largest dimension of each fragment was measured to the nearest millimeter to characterize the size of the substrate material at each reef elevation. This analysis was not repeated on the Fisherman's Island reefs.

Dead oysters collected from Goodwin Islands were examined for evidence of predation by crabs in 2000 and

2001. Predation by crabs on oysters was distinguished from other sources of mortality by the presence of chipped or cracked valve margins, puncture holes within the umbo region, crushing of the umbo region, and complete crushing of the valves. This analysis was not repeated on the Fisherman's Island reefs.

Statistical Analysis

Differences in oyster densities among reef elevations (base, flank, and crest) and among sampling times (November 1999, July 2000, June 2001) at the Goodwin Island reef were assessed by two-way full-factor fixed effects model analysis of variance (ANOVA). Separate ANOVAs were conducted for small (≤ 30 cm shell height) and large (> 30 cm shell height) live oysters and for identical categories of dead oysters to independently examine the effects of elevation and date on juvenile (small) and mature (large) oyster survival. Cochran's test was used to test for homoscedasticity of variances. Square root transformation of the data was not sufficient to meet the assumptions of the ANOVA, so density values were log transformed [$\ln(x + 1)$] to conform with homogeneity and normality assumptions when necessary. Student-Newman-Keuls (SNK) a posteriori tests were used to explore differences among means when significant factor effects were detected (Underwood 1997).

Differences in live oyster densities among reef elevations, substrate types, and sampling times at the Fisherman's Island reefs were assessed with separate three-way ANOVA models with year, reef type, and elevation as factors. Heteroscedastic variances were corrected with a $\ln(x + 1)$ transformation.

Oyster populations on the reefs at Fisherman's Island were not compared statistically with that of the Goodwin Island reef because of the confounding effects of temporal difference in reef construction and considerable dissimilarities in reef surface area and tidal and salinity regime exposure.

Results

Goodwin Island

Oyster densities on the Goodwin Island reef showed a clear pattern relative to reef elevation at all sampling times with the base of the reef having greater oyster densities than reef crest (Figs. 2 & 3). Elevation on the reef, but not date, influenced densities of both live and dead mature oysters (>30 mm) (Table 1). These oysters were significantly more abundant at the reef base compared with the flank and crest (Fig. 2). The size of clamshell fragments making up the reef substrate reflected the distribution of larger oysters and varied among elevation strata (ANOVA, $p < 0.001$). SNK a posteriori tests ($\alpha = 0.05$) revealed that fragments of clamshell were significantly larger at reef base compared with flank and crest. Shell fragments from the flank and crest did not differ significantly.

Densities of live juvenile oysters (≤ 30 mm) were significantly affected by reef elevation, date, and their interaction ($p = 0.007$) (Fig. 3). SNK tests performed to decouple the cause of the elevation \times date interaction revealed: (1) during the 1999 and 2000 sampling events, densities of

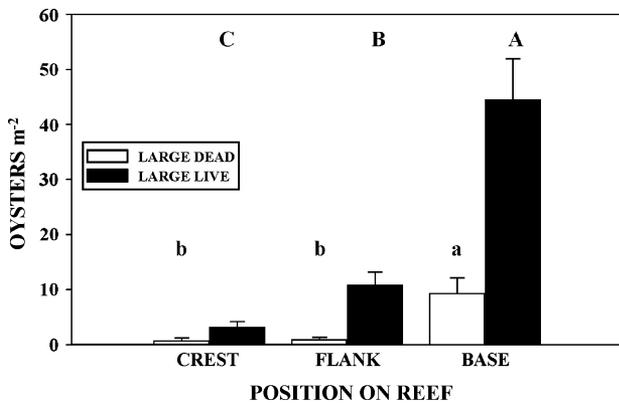


Figure 2. Mean density of large (>30 mm shell height) live and dead (nonfouled, articulated oyster shells only) oysters at the crest (1.5 m above the seabed), flank (0.8 m above the seabed), and base (0.2 m above the seabed) of the Goodwin Island created oyster reef, York River, Virginia in 1999, 2000, and 2001. Bars represent mean abundance per square meter + 1 SE ($n = 6$). Separate ANOVA and SNK a posteriori tests were used to compare densities of live and dead oysters. Because there was no significant effect of sampling date, data shown are pooled from all sampling events. Letters above bars represent results of SNK a posteriori comparisons: dead: $a > b > c$, live: $A > B > C$, $\alpha = 0.05$.

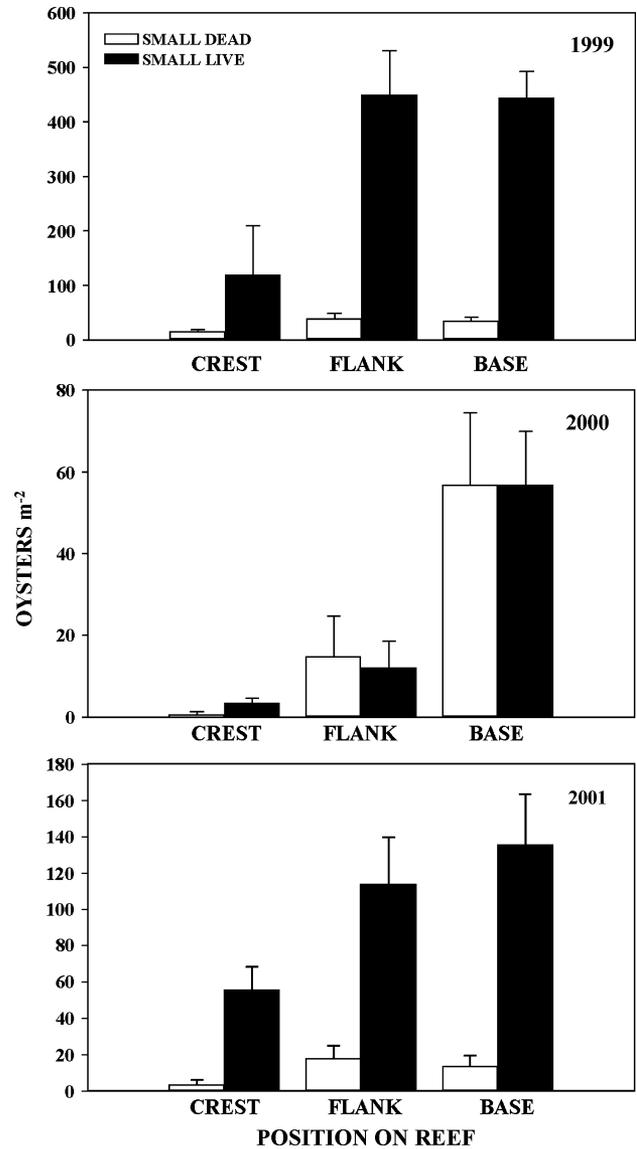


Figure 3. Mean density of small (≤ 30 mm shell height) live and dead oysters (*Crassostrea virginica*) at the crest (1.5 m above the seabed), flank (0.8 m above the seabed), and base (0.2 m above the seabed) of the Goodwin Island created oyster reef, York River, Virginia, November 1999, July 2000, and June 2001. Bars represent mean abundance per square meter + 1 SE ($n = 6$).

small live oysters were greater at the flank and base than densities at the crest; (2) during the 2001 sampling period, no statistically significant difference in juvenile oyster density according to reef elevation was detected, although as in 1999 and 2000, densities tended to be lowest at the crest; and (3) recruitment of juvenile oysters was lowest in 2000 across all elevations. Densities were greatest in 1999 and intermediate in 2001 at both the reef flank and the base, but no significant differences were detected in densities in these years at the reef crest. Densities of dead juvenile oysters (≤ 30 mm) were significantly affected by reef elevation and date (Fig. 3). These oysters were

Table 1. Summary of two-way ANOVA results testing whether oyster densities ($\ln(x + 1)$ transformed) at the Goodwin Islands constructed oyster reef varied as a function of position on reef and date.

	Source	Degrees of Freedom	Mean Square	F	p	Multiple Comparisons
Small dead oysters (≤ 30 mm)	Position on reef	2	19.400	15.19	<0.001	<u>C < F = B</u>
	Date	2	8.960	7.02	0.002	<u>99 < 00 = 01</u>
	Position on reef \times date	4	3.180	2.49	0.056	
	Error	45	1.280			
Large dead oysters (>30 mm)	Position on reef	2	13.203	17.54	<0.001	<u>C = F < B</u>
	Date	2	0.972	1.29	0.285	
	Position on reef \times date	4	0.527	0.70	0.596	
	Error	45	0.753			
Small live oysters (≤ 30 mm)	Position on reef	2	17.790	30.42	<0.001	
	Date	2	39.423	67.42	<0.001	
	Position on reef \times date	4	2.354	4.03	0.007	See text
	Error	45	0.585			
Large live oysters (>30 mm)	Position on reef	2	31.020	26.97	<0.001	<u>C < F < B</u>
	Date	2	1.620	1.41	0.256	
	Position on reef \times date	4	0.930	0.81	0.527	
	Error	45	1.150			

Multiple comparisons of the means were analyzed using SNK tests. Treatments are listed in ascending order of means, and treatments not connected by a common underline differed at $p = 0.05$. Values in bold indicate significant effect (or interaction) at $p < 0.05$. B, base; C, crest; F, flank.

significantly more abundant at the reef base than at the flank and crest (Table 1).

Size frequency distributions reveal that for each of the 3 years (Fig. 4), juvenile oysters (≤ 30 mm) numerically dominated all samples. Reef crest oysters had a unimodal population distribution each year. Flank and base reef strata exhibited bimodal size distributions in 2001. Juvenile oysters dominated all three strata throughout the sampling period, with mature oysters (>30 mm) rare. A

greater proportion of mature oysters were collected from the reef base than from the reef flank, although the difference was small. Dead oysters (with articulated shells) were present at each elevation each year and, although fewer in number, tended to reflect the distribution of live oysters at each elevation.

Dead oysters exhibiting evidence of predation by crabs were collected from each reef elevation but were proportionally more abundant at reef crest and flank compared with the reef base (Fig. 4).

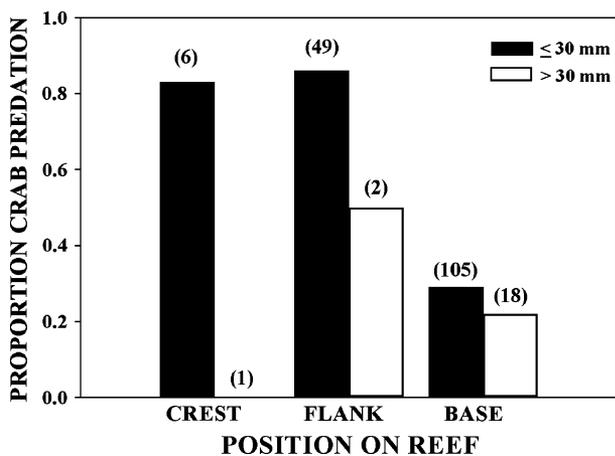


Figure 4. Proportion of dead oysters with evidence of predation by crabs out of total number of dead oysters sampled in 2000 and 2001 from each position on the reef at Goodwin Island. Numbers in parentheses above bars correspond to total number of individuals observed.

Fisherman's Island

The mean density ($\ln(x + 1)$ transformed) of oysters at Fisherman's Island varied significantly according to tidal reef elevation, substrate type, and date (Table 2). There was also a significant tidal reef elevation \times substrate type \times date interaction. This interaction was attributed to oyster density patterns observed on the clamshell reef in 1997 (Fig. 5). Subtidal oyster densities on the clamshell substrate reef were greater than those densities at low intertidal reef elevations in 1997. During all other sampling events on both reef types, oyster densities exhibited the reverse pattern with greater oyster densities at the low intertidal reef elevation compared with those located subtidally (Fig. 5). Densities of oysters increased over time at the subtidal elevation of the oyster shell reefs and at the low intertidal reef elevation of the clamshell reefs (Figs. 5 & 6). This pattern was not evident at the low intertidal reef elevation on the oyster shell reef where the density of oysters was lowest in 1998. Oyster densities

Table 2. Summary of two-way ANOVA of live oyster densities ($\ln(x + 1)$ transformed) from the reefs at Fisherman's Island, Virginia.

Source	Degrees of Freedom	Mean Square	F	p
Elevation	1	17.381	8.97	0.004
Substrate type	1	318.188	164.29	<0.001
Elevation \times substrate type	1	1.290	0.67	0.418
Date	2	20.356	10.51	<0.001
Elevation \times date	2	5.139	2.63	0.079
Substrate type \times date	2	1.291	0.67	0.517
Elevation \times substrate type \times date	2	11.447	5.91	0.005
Error	60	1.937		

Values in bold indicate significant effect (or interaction) at $p < 0.05$.

remained low throughout the study at the clamshell reefs' subtidal elevation (Fig. 5). None of the first order interaction effects were significant (all $p \geq 0.079$) (Table 2).

Oysters were consistently more abundant on the oyster shell than on the clamshell reef habitat. Overall abundance patterns on clamshell were similar to that found on the clamshell reef at Goodwin Island with a population dominated by small oysters and few oysters surviving to larger sizes (>30 mm) (Fig. 6). By May 1997, nearly 1 year after reef construction, oysters were notably more abundant on the oyster shell reef compared with the clamshell reef. By May 1998 and through 1999, the size distribution of oysters on the oyster shell reef was bimodal with relatively large numbers of larger live oysters, whereas a weaker bimodal size distribution of small live oysters, likely masked by low recruitment, was found on clamshell (Fig. 6). Recently, dead oysters with articulated shells were present on both reef types all years and tended to reflect the distribution of live oysters. There appeared to be increased survival on the oyster shell habitats because the ratio of live oyster to recently dead oyster abundance was greater on the oyster shell reefs than on the clamshell reefs each year.

Discussion

Observed Patterns in Oyster Densities

This study compared the development of oyster populations on different cultch materials in intertidal and subtidal settings. The ultimate formation of a living veneer of oysters over the core base material is partly dependent on the success of the substrate material to support survival and growth of the initial cohort of oysters that recruit to the constructed reef.

The bases at the subtidal Goodwin Island and intertidal Fisherman's Island reefs developed quite different oyster populations on similar substrate materials under different physical regimes and recruitment levels. Although the York River has been characterized by low recruitment in recent years (Morales-Alamo & Mann 1996, 1997, 1998; Southworth et al. 1999, 2000, 2001), juvenile oysters recruited to the Goodwin Island reef each year. Spawning

of *Crassostrea virginica* is initiated by temperature (20–25°C) (Galtsoff 1964) or salinity cues (>10 practical salinity unit [psu]) (Abbe 1986) and typically occurs between June and October in lower Chesapeake Bay (Andrews 1951). Although low oyster recruitment has been prevalent in Virginia since 1991 (Southworth et al. 2000), the relatively high number of recruits observed in 1999 at the Goodwin Island reef compared with subsequent years likely resulted from temporal differences in sampling events. In 1999, the reef was sampled in November, after the conclusion of the settlement period, so the population reported here included young oysters recruited to the reef during the summer of 1999. During the other 2 years, the reef was sampled in the summer at the beginning of reproductive activity and data reflect the oysters that survived through the previous winter as well as some of the early recruits of that year. A recruitment event of the magnitude observed in November 1999 was not observed again in 2000 or 2001, nor was it reflected in the number of small oysters observed in subsequent years.

Oyster densities on both substrate types steadily increased over time at Fisherman's Island but the population on the oyster shell far exceeded that on the clamshell mound. By 1999, the single oyster shells that made up the base of the reef were encrusted by a continuous veneer of live oysters. This veneer never formed on the clamshell mounds.

Possible Processes Driving the Patterns Observed

Low recruitment on areas comprising small substrate components (the clamshell reefs at Fisherman's Island and the crest and flank of the Goodwin Islands reef) compared with reef areas of larger reef material fragments (Fisherman's Island's oyster shell reefs and the base of the Goodwin Island reef) may be attributed to differential substrate selection by oysters at the larval stage and post-settlement loss. The former, as evidenced by reduced initial settlement, could be a result of physical processes such as turbulence and flow. If settlement and metamorphosis success were unequal across substrate types, surviving oysters could be expected to be more abundant on reefs with favorable larval habitats, such as demonstrated by the

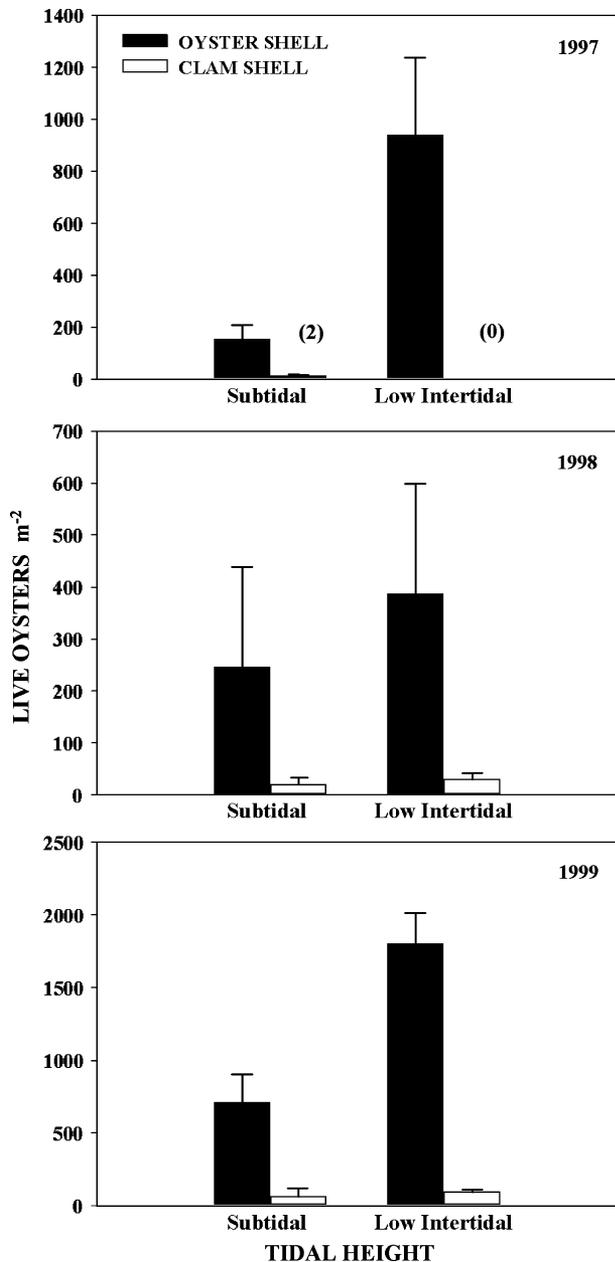


Figure 5. Mean density of live oysters at subtidal and low intertidal (mean low water) elevations on constructed oyster shell and clamshell intertidal reefs at Fisherman's Island, Virginia over 3 years. Bars represent means + 1 SE ($n = 6$). Numbers in parentheses in the top panel represent mean oyster abundance on clamshell substrate.

patterns observed on the oyster shell of Fisherman's Island or larger clamshell fragments at Goodwin Island. Conversely, if oyster larval settlement and metamorphosis success were equal across all reefs, the patterns observed could be a result of differing post-settlement mortality pressure on different reef types. If this post-settlement mortality was the result of predation, then different reef substrates may foster predator communities imposing different pressures on newly settled oysters. The matrix of

the oyster shell reef substrate, having larger interstitial spaces compared with clamshell (O'Beirn et al. 2000), could be more accessible to fish and decapod predators. Although these larger predators may not prey directly upon the small, new recruits, they may feed upon smaller, intermediate predators of oysters, making the reef matrix a predation refuge for young oysters (McDermott & Flower 1952; Grabowski 2004). Smaller interstitial spaces, such as those of the clamshell substrate, may be limiting to larger predators but accessible to small decapods (such as juvenile panopeid and portunid crabs) and flatworms. This reef type may serve as a structural refuge for these individuals, permitting grazing on newly settled oysters. The resulting oyster population would reflect these trophic interactions with few oysters persisting on clamshell substrates. No direct predation comparisons were made between clamshell and oyster shell reefs at Fisherman's Island during this study, hence, further examinations of interactions of newly settled oysters and their predators on different substrate materials are needed to elucidate the potential importance of habitat selection and predation processes in structuring these communities.

The geometry of the reef substrate cultch material and the extent of predation refuge it affords can also explain the differential survival of oysters and the observed oyster abundance patterns on different substrate materials. Decapod predators, including the Blue crab (*Callinectes sapidus*) and Panopeid mud crabs (i.e., *Panopeus herbstii*, *Dyspanopeus herbstii*, *Eurypanopeus depressus*), are major predators of bivalve mollusks and can cause high levels of mortality in juvenile oyster populations (McDermott 1960, Krantz & Chamberlin 1978; Seed 1980; Bisker & Castagna 1987; Eggleston 1990; reviewed by White & Wilson 1996; Grabowski & Powers 2004). Fragile shells of young oysters (<15 mm shell height) are susceptible to crushing by these predators. Crabs generally chip the margins of the valve of larger oysters with their chelae to gain access to the tissue inside. The vulnerability of a given oyster to decapod predation is a function of oyster shell height and thickness, oyster growth geometry, and the site of attachment on cultch material (Eggleston 1990). An oyster attached to the cupped depression on the nacreous surface of the cultch shell is less likely to be successfully preyed upon by crabs because the depression limits the crab's ability to reach the oyster with chelae and protects the oyster from crushing (Eggleston 1990). In laboratory experiments, larger oysters (>30 mm shell height) were less likely to be successfully preyed upon by the Blue crab, *C. sapidus* due to increased shell thickness compared with smaller oysters (Eggleston 1990).

Structurally complex habitats typically support dense, diverse faunal assemblages and can influence predator-prey dynamics (Menge & Sutherland 1976; Orth et al. 1984). Experimental studies have demonstrated that habitat complexity reduces predator foraging efficiency by reducing the predator-prey encounter rate (Bartholomew et al. 2000; Grabowski 2004). In addition to influencing

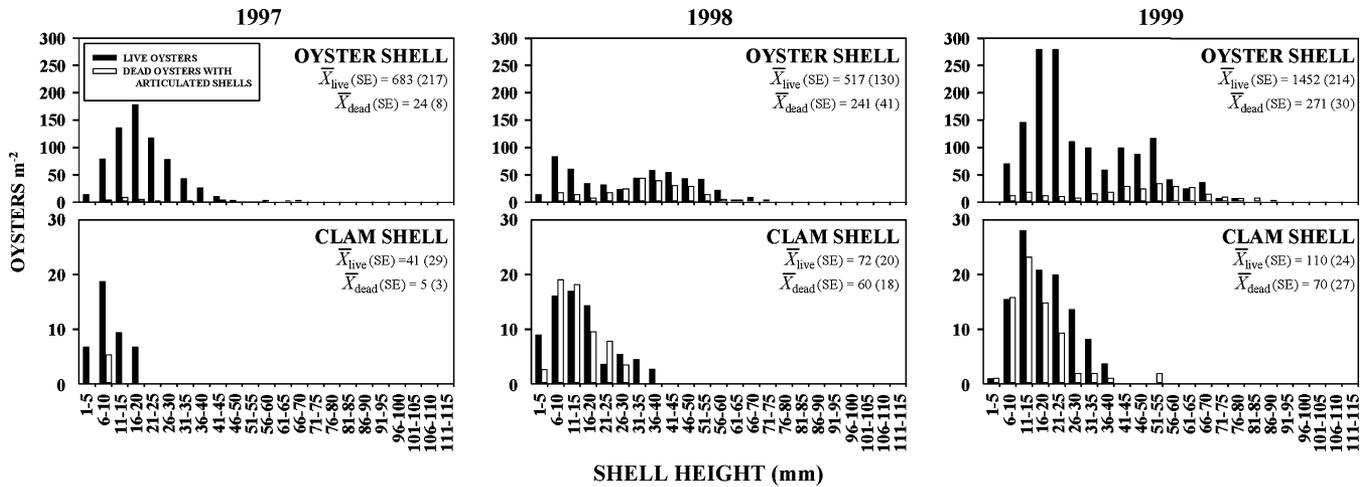


Figure 6. Size frequency distributions for live and dead (nonfouled, empty articulated oyster shells) oysters collected from oyster shell and clamshell reef mounds at Fisherman’s Island, Virginia in May 1997, 1998, and 1999. Bars represent mean oyster densities for each size class and are for all animal combined from three replicate quadrat samples (0.0625 m²) collected from each of two clamshell reefs and one oyster shell reef at three tidal heights (0.25 m below mean low water, at mean low water, and 0.25 m above mean low water) and one oyster reef at two tidal heights (0.25 m below mean low water and at mean low water).

trophic dynamics, structurally complex habitats may also enhance food deposition and larval settlement by baffling water movements (Commito & Rusignuolo 2000). Bartol et al. (1999) underscore the importance of interstitial space within the fabric of intertidal reefs to promote oyster survival during periods of severe temperature extremes. Given these factors, the material used to construct oyster reef bases in restoration efforts should afford appropriate architectural complexity.

The small-scale structure of reefs appears to be important in enhancing the value of the habitat for oyster settlement. Substrate material with ample convolutions and interior surfaces for settlement out of direct reach of decapod predators gives young oysters a survival advantage not afforded to those that settle on less suitable substrates. Areas on the reef where the substrate consists of small, tightly packed shell fragments, where the substrate does not offer adequate shelter from predation, can leave young oysters vulnerable to crab predation. For example, the distribution of oysters with evidence of crab predation reflected the size distribution of clamshell fragments on the reef mound of the Goodwin Island reef. Proportionately fewer dead oysters (regardless of size) displaying typical evidence of crab predation (Eggleston 1990) were collected from the base of the reef where the substrate afforded adequate refuge for young oysters from predators. We suggest that the dead oysters collected here succumbed to other sources of mortality, such as disease (Ragone Calvo & Burreson 2000, 2001, 2002) and flatworm predation (Abbe 1986; Newell et al. 2000).

In reefs or regions of reefs comprising substrate material that did not offer adequate shelter from predation, mortality of young oysters from decapod predation

likely occurred before disease infection could kill the oyster. Of the two substrate materials evaluated, oyster shell may provide more available settlement surfaces with room to grow and adequate water flow to supply food to young oysters compared with clamshell.

Physical disturbance, through the mechanical grinding of the substrate material by waves and currents, may partially explain distribution of live oysters and the physical structure of the subtidal reef at Goodwin Island. The structure of this reef is analogous to natural mature subtidal oyster reefs of the Gulf Coast exhibiting the “grit principle” (MacKenzie 1977; Gunter 1979). Reefs of this type form barren central ridges consisting of fine dead shell grit on the reef crest and live oysters are only found along the flanks and in deeper water. Constant motion of the crest substrate from effects of wind-generated waves and currents abrades sessile organisms and hinders oyster larvae development (Gunter 1979). Because few live oysters were collected at the reef crest, which was made up of small, unconsolidated broken shell fragments, such physical disturbance may partially explain the distribution of oysters observed on this reef, which is opposite of that described by Lenihan et al. (1996) on constructed reefs in North Carolina.

Restoration Implications

Because efforts to restore oyster reefs become more widespread along the Atlantic coast, we learn that there is no generic model for construction and configuration of the reefs (e.g., size, shape, vertical relief, substrate type). The results of this study further affirm the importance of substrate complexity in the development of oyster

populations on restored reefs reported in earlier studies (Bartol & Mann 1999; Bartol et al. 1999; O'Beirn et al. 2000), but they also highlight the importance of environment-specific interactions and point to the need for improved understanding of the mechanisms affecting the interaction between substrate characteristics and oyster recruitment and survival. Constructed reef design should account for local geophysical and biological conditions and provide shelter for oysters and associated fauna from such stressors as hypoxia, siltation, ice scour, and resident and transient predators.

Materials used as reef substrate should provide adequate small-scale structural complexity with ample refugia for newly settled oysters to avoid predation, whether subtidally or intertidally. An effect of substrate material used in the construction of oyster reef habitats was observed on the subsequent abundance of oysters on these habitats. Results from this study indicate that the interstitial space afforded by the material used to construct the reef contributes to the ability of oysters to escape predation and survive. Therefore, considerations of small-scale structural design, such as the availability of proper settlement substrate (i.e., adequate surface heterogeneity), may be more important to the success of reef restoration efforts in some settings than large-scale aspects of reef design, such as mounding vertical relief. Oyster shell and large fragments of clamshell provided sufficient habitat to support and sustain a viable oyster population. Large-scale vertical relief extending up into the intertidal may not be as important in shallow (<2 m), subtidal habitats with good water quality and low sedimentation as is proper settlement substrate.

Given the limited supply of oyster shell for restoration, the results of this study should be used to reassess the types of material and reef construction configurations in future oyster reef restoration efforts. Rather than building an entire mound of one substrate material, a mixture of substrates may lead to improved restoration success. Less desirable substrate materials, such as small Surf clamshell fragments (this study) or gravel (Soniat et al. 1991), could be placed as a base within the core of the mound, and then covered by a veneer of a material comprising larger elements (such as oyster shell, if available, or whole clamshell valves), which offers greater habitat complexity. Because the settlement of oyster larvae is often restricted to the outer layer of substrate material on a reef base (Bartol & Mann 1999), a practical construction approach would be to limit preferred substrate materials to the areas available for settlement. This layer could then provide the small-scale surface structural complexity to the peripheral strata of the mound, providing ample convolutions or tortuosity and surface area to afford settlement surface and refuge for young oysters from predation and physical stress. Thus, the choice of an appropriate construction configuration and substrate type for use as a reef base can dictate success or failure of the developing reef assemblage.

Implications for Practice

- Given the limited supply of oyster shell for reef restoration activities, Surf clamshell is a practical alternative when certain design considerations are followed.
- Results of this study indicate that the small-scale structure of constructed reefs appears to be important in enhancing the value of the habitat for oyster settlement.
- The design and materials used for restoring oyster reefs influences the basic ecology of the restored system.

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