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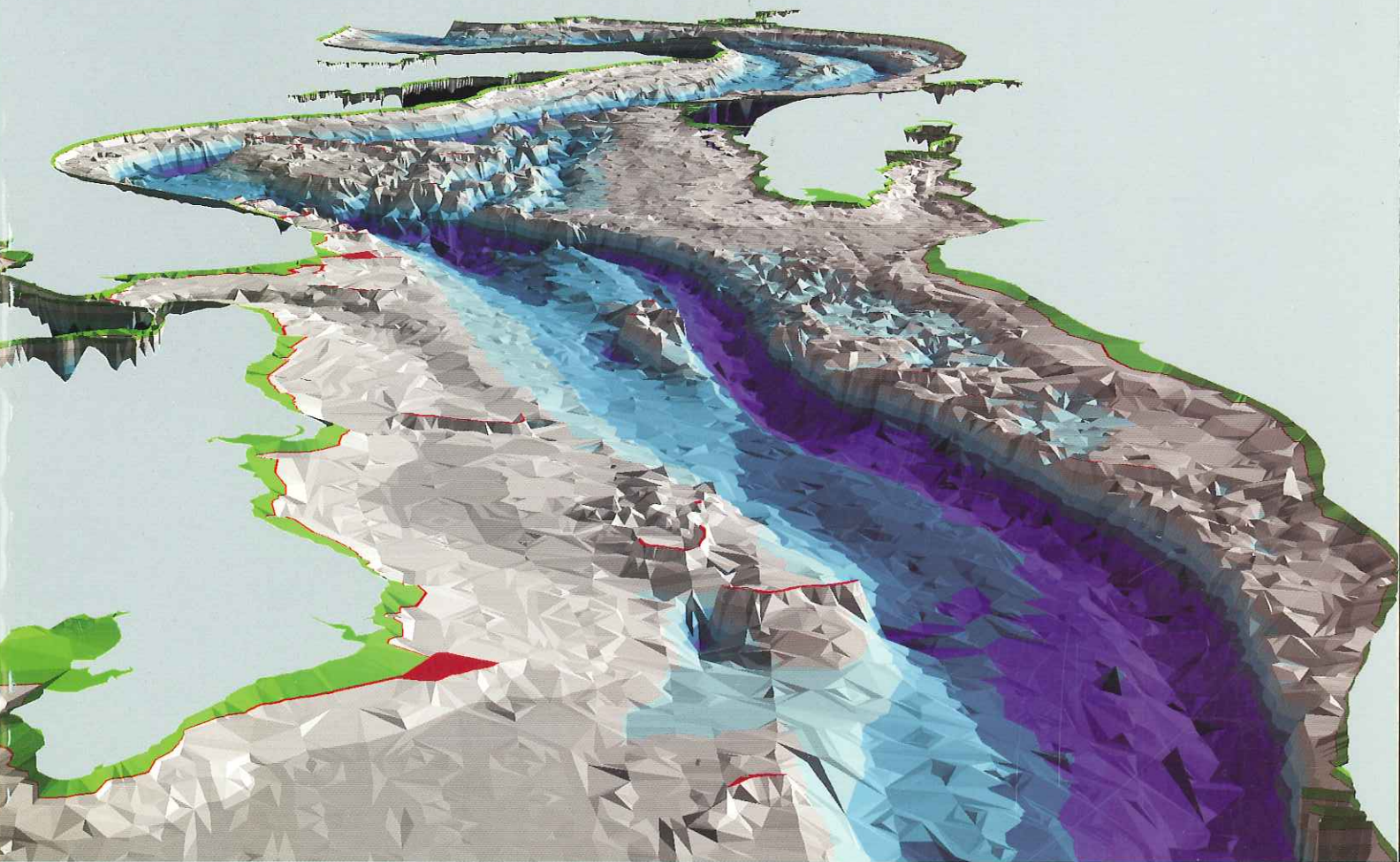
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Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches

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Editors



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**Small-Scale Patterns of Recruitment On
A Constructed Intertidal Reef:
The Role of Spatial Refugia**

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Abstract

Traditional oyster repletion activities have utilized a two-dimensional approach to shell (substrate) deployment to attain maximal coverage in subtidal locations with little consideration for optimal thickness of deployed shell and tidal elevation. Vertical dimensionality may play a vital role, however, in the establishment and persistence of oyster communities. Therefore, a three-dimensional oyster reef was constructed in the Piankatank River, Virginia, and settlement and mortality patterns of oysters were recorded from June of 1993 through September of 1994. The reef was constructed entirely of oyster shell on the footprint of an historical reef, and extended from 2.5 m below mean low water (MLW) to 0.75 m above MLW. The reef covered an area approximately 150 x 30 m, with numerous sections, varying from 2 - 20 m² in area, exposed at low tide. In both intertidal and subtidal locations settlement and subsequent mortality (recruitment) were monitored both at the surface of the reef shells and within the interstices of the reef at depths of 10 cm. Settlement was greater in subtidal locations, and no difference in settlement intensity between surface and subsurface environments was detected. Survivorship rates along the intertidal-subtidal continuum varied temporally, but for most of the year, were highest at MLW, where physical and predatory influences rarely are that severe. Oysters which attached to subsurface substrate benefitted primarily from refugia from temperature extremes in intertidal locations and from relief from predation in subtidal environments. We suggest the moderation of these biological and physical stresses both within the reef interstices and within the low intertidal zone plays an instrumental role in increasing survival: even minor submergence within the reef and small changes in vertical elevation provide relief from scorching summer and freezing winter air temperatures and furnish protection from predators, most notably crabs and flatworms. In practical terms these results proffer an important lesson: both reef tidal elevation and substrate thickness provide microscale refugia for settlement and survival of early oyster life history stages.

Introduction

Traditional oyster replenishment programs have focused on spreading thin veneers of substrate suitable for larval settlement over coastal and estuarine bottoms or over foundations of less ideal substrates to maximize areal coverage. In general, such activities have been driven by the practicality of deploying very large volumes of shell, a commodity of increasing value, at greatest cost efficiency and with reasonable speed, usually with the subsequent intent of retrieving either juvenile (seed) oysters or market size oysters. The end product of this approach, a two-dimensional subtidal carpet of shell and live oysters, has little resemblance to the intricate, three-dimensional reef communities that often extended out of the water at low tide and that oysters once formed naturally in the Chesapeake Bay before man's intervention (Hargis 1997). In light of rapidly declining oyster stocks in the Chesapeake Bay, a concerted effort to re-establish natural oyster communities by constructing artificial reefs has been made by repletion agencies. The ultimate goal of such projects is to rejuvenate dwindling local oyster populations.

Presently, we know little about constructing reefs which are most advantageous for oyster settlement and survival. From the cumulative literature on oyster biology, we know that reefs grew by accretion over time periods of hundreds to thousands of years in a process aided substantially by the preferred settlement of metamorphically competent oyster larvae on shells of the adult oyster. We also know that the physical environment, in the form of currents, tides, and sedimentary forces, practically dictate the perimeter size and the features of the reef. However, we remain ignorant of a number of details, and as a result, there are a number of practical questions, fundamental to an organized approach to reef construction, which are without answers. For example, for a known location what size and shape should the reef be, and can we obtain guidance on this question from current "footprints" of formerly intertidal reefs? Is tidal elevation an important factor to consider

when constructing reefs? Given that shell is a valuable commodity, can other substrates be used to construct reefs? How thick should substrate layers be and how should they be applied?

In this study, we focus on the issues of substrate thickness and tidal elevation. Naturally forming reef systems have some degree of vertical dimensionality that allows for the settlement and subsequent survival of dense populations of oysters at distinct bands along the tidal continuum. Furthermore, natural reef environments have numerous interstitial microhabitats that offer both physical and biological refugia. Both tidal elevation and interstitial habitats may play integral roles in artificial reef ecosystems as well, and may be important factors to consider when constructing reefs for rejuvenation efforts. Thus, within a constructed reef setting, we have set out to determine if 1) tidal elevation influences oyster recruitment processes (settlement and subsequent post-settlement survival); 2) if subsurface interstitial environments are beneficial for survival; and 3) if oysters are even capable of settling within these environments when reefs are constructed of oyster shell. Specifically, we address these areas by measuring settlement and post-settlement mortality of *Crassostrea virginica* at two substrate levels (reef surface and 10 cm below reef surface) and at various tidal heights ranging from +30 cm above mean low water (mid/high intertidal zone) to -90 cm below MLW (mid subtidal zone) on a constructed intertidal reef.

Methods

STUDY SITE

The study was conducted in the Piankatank River, a subestuary of the Chesapeake Bay located in Virginia, at a site which once supported a highly productive natural intertidal reef system, but at the time of reef construction, contained only a remnant shell footprint of the natural pre-existing reef (Fig. 1). The Piankatank River is ideal for artificial reef construction because it once supported a pro-

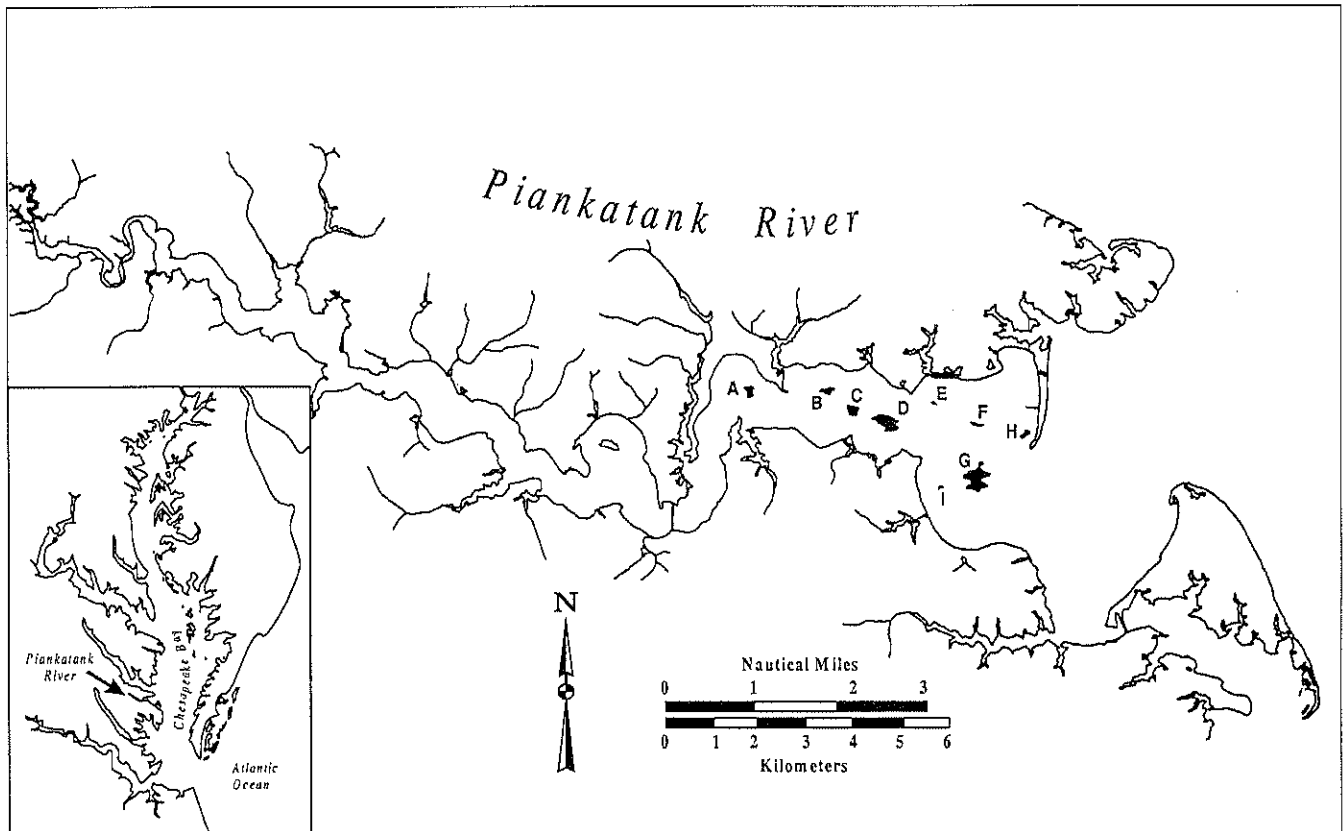


Figure 1. Map of Piankatank River showing the site of reef construction (D) and location of other nearby oyster reefs (A, B, C, E, F, G, H, I)

ductive adult oyster population, has a high abundance of oyster settlement (Morales-Alamo and Mann 1996), there is no commercial oyster fishery, and there is virtually no industry or agricultural development within the watershed. During the course of this study, water temperature at the site varied from 0.5 - 30 °C, salinity ranged from 8 - 20 ppt, and tidal range was small (mean range = 36 cm).

REEF CONSTRUCTION

The reef was constructed in June 1993 by the Virginia Marine Resource Commission (VMRC). The construction procedure involved the deployment of aged oyster shells from barges using a high pressure hose. The shells were discharged in an area approximately 150 x 30 m, which were the approximate footprint dimensions of the historical reef. After completion, the reef consisted of numerous sections, varying from 2 - 20 m² in area, exposed at low

tide, and extended from 2.5 m below mean low water (MLW) to 0.75 m above MLW. The majority of the reef, however, did not extend much deeper than 1.0 m below MLW or much higher than 0.35 m above MLW.

SAMPLING PROCEDURE

The reef was sampled in both 1993 and 1994. During the 1993 sampling period 2 of the 12 principal intertidal hummocks comprising the reef system were focused on: one on the reef periphery completely exposed to wave action and currents and a second situated near the middle of the reef partially shielded from wave action and currents. These hummocks were sampled using a transect approach, whereby samples were collected along upstream and downstream transects on each of the two mounds during each period of sampling. Transects were carefully marked on the reef to prevent resampling. Along each transect four

tidal heights were considered: 30 cm above MLW, MLW, 45 cm below MLW, and 90 cm below MLW.

During the 1994 sampling period, after data from the previous year were analyzed and we had a preliminary understanding of the reef system, a randomized approach was used which was more geographically expansive and statistically powerful. In this method, eight hummocks were partitioned into 64 x 20 cm plots using rope and reinforced bars, and experimental sites were selected randomly across all eight mounds. Four of the 12 primary hummocks were not considered because ice scouring during the '93-'94 winter eroded the hummock apices, resulting in the loss of substantial intertidal substrate. In this randomized approach, three tidal heights were considered: 25 cm above MLW, MLW, and 90 cm below MLW. The high intertidal height was lowered slightly to accommodate as many intertidal hummocks as possible in the sampling procedure, and one of the subtidal heights, 45 cm below MLW, was eliminated to incorporate more replication. In addition to tidal height another factor, substrate level, was considered. To document the effects of substrate level, samples were collected both at the reef surface and 10 cm below the reef surface.

During both years of sampling, non-destructive and destructive sampling were employed from June through September to assess settlement/early recruitment within the reef ecosystem. Non-destructive sampling involved the weekly placement of oyster shells in open-topped, 64 x 20 cm, rubber coated 1 inch wire mesh trays secured to the reef surface by reinforced bars. In 1993 a surface layer of 20 shells was placed weekly in single level trays which were fixed spatially to the reef at all four tidal height designations along upstream and downstream transects at each of the two mounds. The concave and convex side of all 20 shells within individual cages were examined for recently settled oyster larvae (spat) using a dissecting scope, and a spat total per cage was recorded. In 1994 three-tiered trays containing 30 shell upper and lower levels, which were spaced 10 cm apart, and a 40 shell intermediate level were

buried into the reef substrate until the upper level was even with the reef surface. Each week trays were placed at 12 different, randomly selected plots (four plots for each of the three tidal heights). Both surfaces of shell found in the upper and lower tiers were examined for spat, and a surface layer spat total and a deep layer spat total were recorded at all 12 weekly selected plots.

Destructive sampling involved the weekly placement of 64 x 20 cm quadrats on the reef surface, the removal of a layer of shell, and the subsequent examination of both shell surfaces for spat. This sampling technique provided an index of cumulative spatfall on the actual reef substrate and accounted for any early post-settlement mortality losses. In 1993 the quadrats were placed at all four tidal heights along upstream and downstream transects chosen on each of the two mounds. To prevent resampling, successive samples collected over time were taken along transects which were immediately adjacent to previously sampled transects. During this period only a surface layer spat total per plot was calculated. Plots used in 1994 destructive sampling were selected randomly across all eight remaining intertidal mounds. As with 1994 non-destructive samples, four plots were selected randomly each week at all three tidal heights. At each plot, a surface layer of shell and a layer 10 cm beneath the reef surface, easily distinguishable from the surface layer by its brown detrital film, was extracted and examined for spat. This allowed for the calculation of both weekly surface and weekly deep spat totals for all 12 plots.

To determine if oysters which settled along these spatial gradients would survive, oysters of various age classes were tracked throughout the fall, winter, and summer months. On August 12, 1993, oyster larvae were set on clean oyster shells in densities of 5-25 spat per shell at the Virginia Institute of Marine Science Oyster Hatchery. Shells containing spat were placed in Vexar mesh bags (100 shells per bag), and spat were reared in hatchery systems to sizes comparable to oysters found on the reef. On September 26, 1993 the mesh bags were placed on the

reef at the same 4 tidal heights designations used in the 1993 settlement monitoring program along two distinct transects on each of the two hummocks. On October 14 and November 11, 1993, and May 5, 1994 25 shells were haphazardly selected from each bag, which was shaken vigorously prior to selection, and shells were photographed with an Olympus OM camera equipped with a 50 mm macro lens. Recent spat scars on each shell were noted and proportional mortalities (# scars per shell / # live oysters at the start of each sampling period) were calculated.

Over the summer of 1994, a different method that considered all intertidally exposed hummocks at the reef site and two year classes of oysters was used to document mortality. One year class consisted of hatchery oysters set on oyster shell on May 16, 1994 in the VIMS Oyster Hatchery, whereas the other year class consisted of a well mixed sample of oysters used in the previous experiment. For each year class, 30 oysters present collectively on 15 randomly picked shells were numbered using paint markers and were placed on either the upper or lower level of 32 x 20 cm, three-tiered, 1 inch mesh cages. Both upper and lower levels, which were 10 cm apart, were filled with shell containing live oysters, but the middle level was filled with 20 shells devoid of live organisms. To keep densities within the 15 shell assemblages as constant as possible, the physical removal of oysters in high density communities was sometimes necessary.

At each of the three tidal heights considered in the 1994 settlement study, eight plots were selected randomly for each year class. At each plot (2 year classes x 3 tidal heights x 8 plots = 48 total plots), cages were buried into the reef substrate until the upper layer was even with the reef surface. The cages were held in place with a reinforced rod. Photographs of labelled oysters were taken in the field with a Nikonos V camera equipped with a close-up lens and focusing frame at 28 day intervals in June, July, August, and September. Estimates of the number of blue crabs and mud crabs present within the upper and lower tiers of each cage were

recorded in the field, whereas the number of flatworms present within the two levels were measured from photographs. To enhance photographic clarity and reduce fouling, a 3 HP gasoline powered Homelite water pump was used in the field to clean labelled oysters and cages. Proportional mortality values per layer of each cage were computed for each sampling interval.

STATISTICAL ANALYSIS

The argument may be made that 1993 settlement and mortality samples collected over time were not independent, since successive samples were taken from either spatially fixed areas, spatially connected plots, or from the same population of organisms. To account for this, analyses of variance (ANOVA) with repeated measures on time were performed on each data set. To satisfy assumptions of homogeneity, all settlement data were $\log(x+1)$ transformed and proportional mortality data were arcsine transformed. When no significant interactions between the within factor, time, and any other factor were detected, 3-way fixed factor (factors: tidal height, mound, and time) ANOVAs were performed. Significant main effects were examined using Student-Newman-Keuls (SNK) tests.

Linear correlations were performed first on surface and deep samples collected in the 1994 settlement and mortality studies to determine if a relationship existed between the two substrate levels. If no significant relationship was detected in the correlation analysis, substrate level was treated as a factor in further statistical procedures. When significant relationships were detected, paired sample t-tests were used to determine if differences existed between surface and deep samples. A mean value for surface and deep data was calculated when no significant difference between the substrate levels was detected, and further analyses were performed on these mean values.

ANOVAs were performed on 1994 non-destructive and destructive $\log(x+1)$ transformed settlement data, and all differences

between means were revealed using SNK multiple comparison tests. Multivariate repeated measures ANOVAs were performed on arcsine transformed mortality data collected in 1994. All significant between factor effects were analyzed using SNK multiple comparison tests, whereas significant within factor effects were examined using Newman-Keuls procedure (pp. 527-528, Winer 1991).

Results and Discussion

The majority of data analyzed in this study suggest that small-scale spatial changes, such as 30 cm shifts in tidal elevation or 10 cm changes in substrate depth, strongly influence the processes of oyster settlement and post-settlement survival. Rather than go into an exhaustive examination of the data, we feel that it would be more constructive (and hopefully more interesting), to present representative examples from the data which illustrate and reinforce key microscale effects within constructed reef settings. For a more comprehensive treatment of the data, please see Bartol and Mann (1997) and Bartol et al. (1999).

Settlement of oyster larvae in a constructed reef environment is heavily dependent on the tidal elevation of the reef substrate. Within the shallow water (≤ 2.5 m) reef system considered in this study, settlement increased with tidal depth. This is most clearly seen in the non-destructive settlement studies, where settlement intensities both in 1993 and 1994 were greatest at -90 cm (Fig. 2). This finding is consistent with several other studies conducted in non-reef environments. For example, greater subtidal settlement rates have been documented by McDougall (1942) using unglazed hearth tiles, Chestnut and Fahy (1953) using clam shells suspended in baskets, and Roegner and Mann (1990) using hatchery-reared larvae exposed to field conditions in microcosms. Nichy and Menzel (1967), who placed oysters on clothmats of mesh within a reef ecosystem, also observed greatest settlement/early recruitment within the subtidal zone.

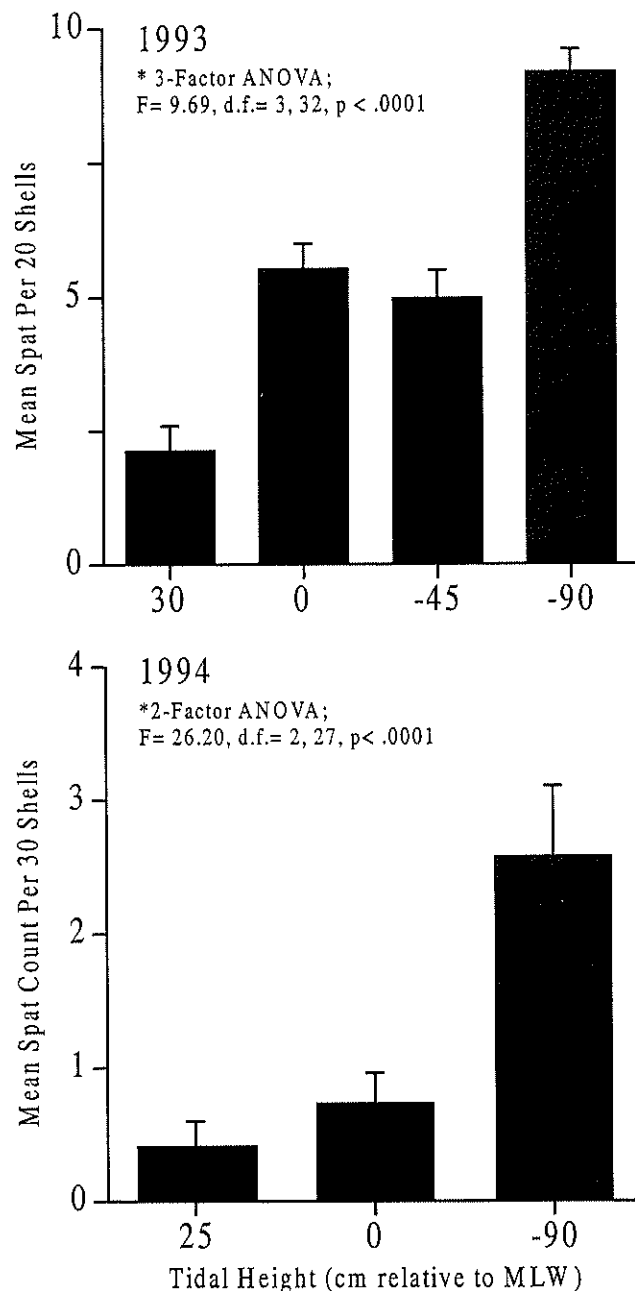
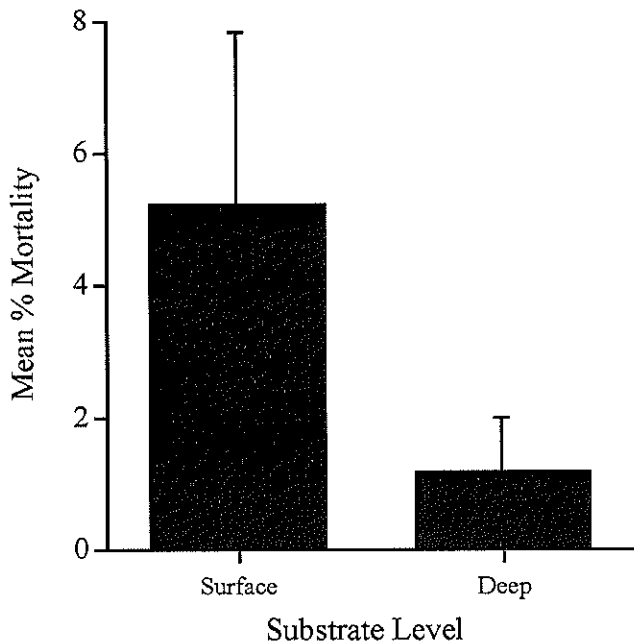


Figure 2. Mean *C. virginica* spat counts recorded in the 1993 and 1994 non-destructive settlement studies. Error bars denote +1 S.E.

The higher rates of subtidal settlement observed in this study were likely a result of several factors. Submergence time may have been one. Oyster larvae in the water column were exposed to subtidal substrates substantially longer than to intertidal substrates, and as a result, had a wider time window in which to set. Submergence time alone, however, did not account for the observed differential settlement. Kenny et al. (1990) found that settlement intensity is not a direct function of submergence



*1-Factor ANOVA; $F=4.86$, $d.f.=1,12$, $p=.047$

Figure 3. Mean percent mortalities of *C. virginica* reared in 1993 residing at the +25 cm tidal height during the June/July sampling period. Error bars denote +1 S.E.

time, especially in the high intertidal zone where settlement is often lower than predicted and the low intertidal zone where settlement is generally higher than predicted. Vertical segregation of oyster larvae in the water column also may have contributed to elevated subtidal sets because oyster late stage pediveliger larvae are more abundant near the benthos than at the surface or within the midwater region (Carriker 1951, Kunkle 1957, Haskin 1964, Baker 1994). Furthermore, because late stage competent to set larvae are negatively phototactic (Cole and Knight-Jones 1939, Ritchie and Menzel 1969, Shaw et al. 1970) and prefer areas of lower wave energy when setting (Ortega 1981, Abbe 1986), they may have actively sought subtidal habitats where light intensities and wave stress are reduced.

Surprisingly, no significant differences in settlement were detected between surface and deep substrates at any of the tidal heights considered (Paired t-tests $> .05$). One concern, however, was that low settlement rates (mean weekly destructive/non-destructive settlement over a three-week settlement period = 0.5 - 3.5 spat per 30 shells) may have dramatically lowered the statistical power of the paired

t-tests. Although this may be a true, a thorough examination of the of the data sets revealed no trend in greater settlement for either substrate depth at any of the tidal heights considered. Therefore, we concluded that larval settlement was not impeded by shell down to depths of 10 cm on artificial reefs composed of oyster shell.

Oyster larvae may have settled 10 cm beneath the reef for a number of reasons. Some of the oyster larvae may have actively attached to subsurface substrate because again they prefer darkened conditions when setting (Ritchie and Menzel 1969) and areas of reduced wave action (Ortega 1981), but also because they seek out environments where flow is low, crevices are abundant, and substrates are not heavily fouled (Abbe 1986, Bushek 1988, Michener and Kenny 1991). A plethora of microhabitats offering reduced flow and sheltered, crevice abundant residence were present within the fabric of the reef, and these habitats were considerably less infested with algal growth and barnacles, altogether making them highly suitable for larval settlement. It is also feasible that because water currents are substantially reduced beneath the reef surface, the interstices served as sediment traps and entrained oyster larvae, which are not thought to be proficient swimmers. Although it is not clear from this study what mechanism, active and/or passive transport of larvae, is responsible for subsurface settlement, it is clear that larvae are capable of settling within the reef interstices and are not impeded by shell down to depths of 10 cm. This is quite remarkable considering that there may be 20 or more shells layers within the 10 cm space.

Although oyster larvae are capable of settling beneath the reef surface, can they survive in these environments? Results from this study suggest that oysters not only survive in these environments, but survive better there during certain times of the year. For example, oysters reared in 1993 that resided at the reef surface at the +25 cm tidal height experienced significantly higher mortalities than oysters residing below the surface from mid June through mid July (Fig. 3). During this period air temperatures were the highest of the year, averaging just

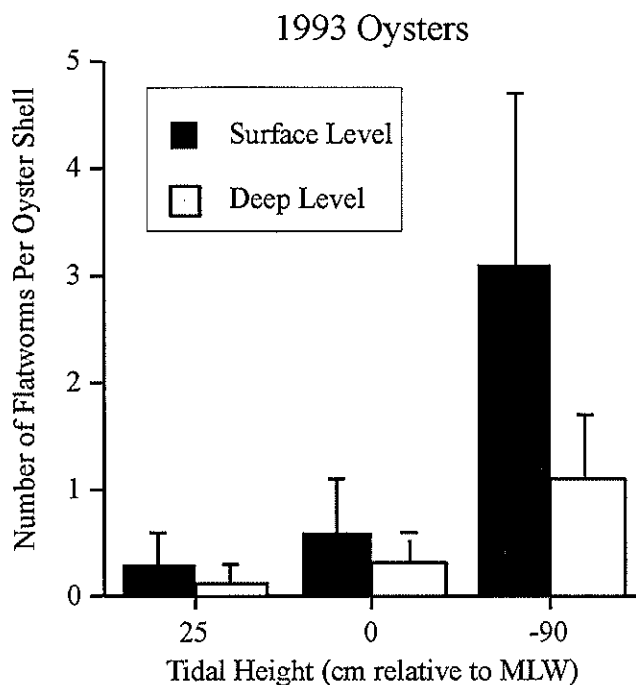


Figure 4. Mean cumulative percent mortalities from June through September, 1994 for the '93 year class oysters residing at the -90 cm tidal height. Error bars denote +1 S.E.

over 28 °C. It is likely that oysters beneath the reef surface benefitted from a shading effect from overlying oysters and shell, and as a result resided in a cooler, moister, more hospitable environment than surface dwelling oysters. In fact, temperature measurements recorded in a subsequent study conducted in July 1995 revealed temperatures 10 cm below the reef surface were 11 °C lower than at the reef surface within the intertidal zone. In natural reefs oysters grow vertically in highly populous clusters, and these aggregated settlements provide mutualistic refuge from solar radiation for all oysters in the community (Bahr and Lanier 1981). Since dense assemblages of vertically growing oysters may take many years to become established, subsurface residence may be critical for the survival of intertidal oysters residing in recently constructed reef systems.

A further example of beneficial subsurface residence is found at the -90 cm tidal height. At this height, significantly higher surface mortalities were detected for oysters reared in 1993 over the entire three month summer

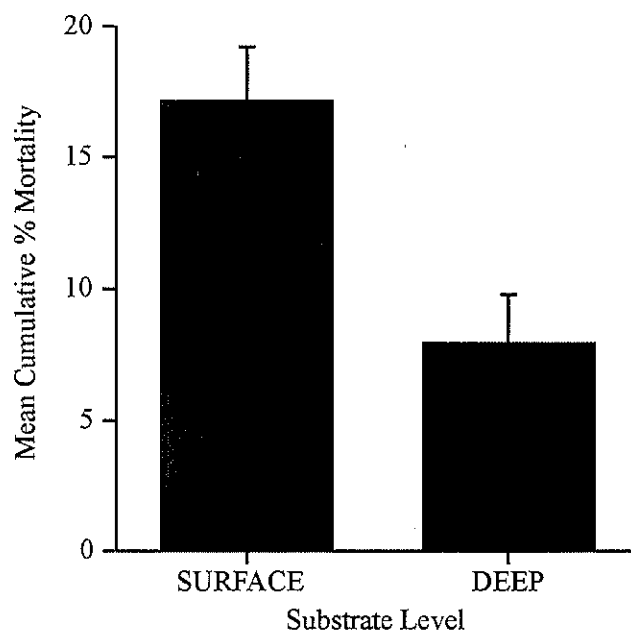


Figure 5. Mean number of flatworms (*Stylochus elliptus*) recorded on shells for the '93 year class oysters residing at three tidal elevations (25 cm above MLW, MLW, and 90 cm below MLW) and two substrate levels (surface, 10 cm below the surface). Error bars denote +1 S.E.

sampling session (Fig. 4). Although the two most deleterious predators, oyster drills and seastars, were absent at the reef site because of low salinities, the flatworm *Stylochus elliptus*, the mud crabs *Panopeus herbstii*, *Eurypanopeus depressus*, and *Rhithropanopeus harrisi*, and the blue crab *Callinectes sapidus* were present, and all are known to contribute to oyster mortality (Landers and Rhodes 1970, Abbe 1986, Littlewood 1988, Eggleston 1990, Baker 1994). These predators were found within cages at surface and deep layers at all tidal heights, but were most abundant at the reef surface and at subtidal depths based on field measurements. For example, in August there was 3.1 ± 1.6 (S.E.) flatworms per shell found on 1993 oysters residing at the reef surface at the -90 cm tidal height, which was more flatworms per shell than any other tidal height/substrate depth designation (Fig. 5). Flatworms and mud crabs were probably the most deleterious because they were highly abundant at the study site and were not restricted by the mesh of the experimental cages. Although adult blue crabs may not have been able to enter the cages, they were able to prey

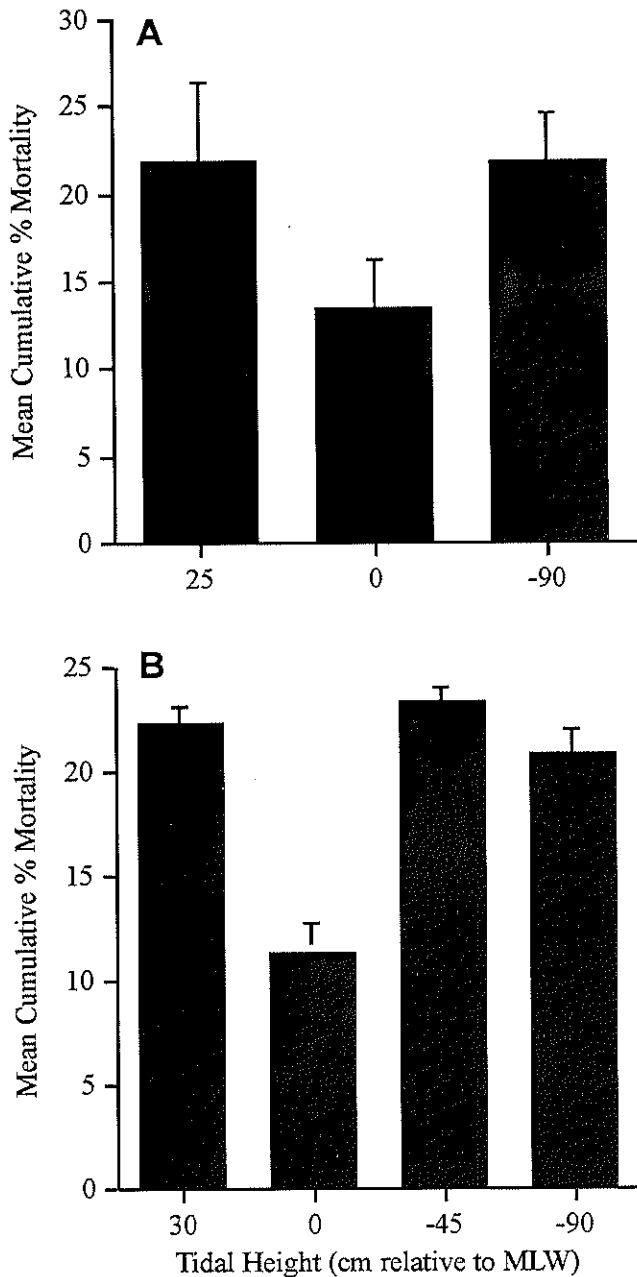


Figure 6. Cumulative percent mortalities for A) the '94 year class of oysters from June-September, 1994 and B) 3-week old oysters from September - November, 1993. Error bars denote +1 S.E.

upon the numerous oysters which grew through the cage mesh.

Of the three tidal heights examined, surface residing oysters survived best at MLW throughout the summer (June-September). For example, oysters belonging to the 1994 year class and dwelling at the MLW tidal height had a cumulative percent mortality of 12 % over the

summer compared with mortalities of 22 % and 23 % recorded at the +25 cm and the -90 cm tidal heights, respectively (Figure 6a). Beneath the reef surface within the reef interstices, there was no detectable difference in mortality along the intertidal-subtidal continuum. This may have been because physical and biological environments were relatively stable within the fabric of the reef regardless of tidal elevation. During the fall oysters situated at MLW had a cumulative percent mortality of 13 %, which again was significantly lower than mortalities recorded at other tidal heights (Figure 6b).

Oysters residing at MLW during the summer and fall probably experienced less predation pressure and fouling than subtidal oysters as a consequence of aerial exposure, but did not suffer from significant heat and respiratory stress like mid to high intertidal oysters because they are not aerially exposed for extended periods of time. This is consistent with the findings of McDougall (1942), Chestnut and Fahy (1953), McNulty (1953), Nichy and Menzel (1967), Arakawa (1980), and Littlewood (1988), where high oyster survival in the mid to low intertidal zone was observed as a result of reductions in predation pressure, physical stresses, sedimentation, and/or competition for space.

Oysters situated at MLW did not fare as well during the winter months. Mortality rates at MLW and higher in the intertidal zone were 95-100 %, whereas mortality rates at the -45 and -90 cm tidal heights were on the order of 25 % (Fig. 7). These mortality rates, especially at MLW, were likely atypical and a result of the coincidence of an unusually brutal winter and the presence of a young population of oysters (oysters were 4 months old at the onset of the winter). From December of '93 through March of '94 air temperatures dropped below freezing 28 days, which is very unusual for Virginia. Oysters less than 1 year old are especially vulnerable to freezing conditions because they put much of their energy into growth and maintenance rather than into the storage of glycogen, a preferred substrate for anaerobic respiration,

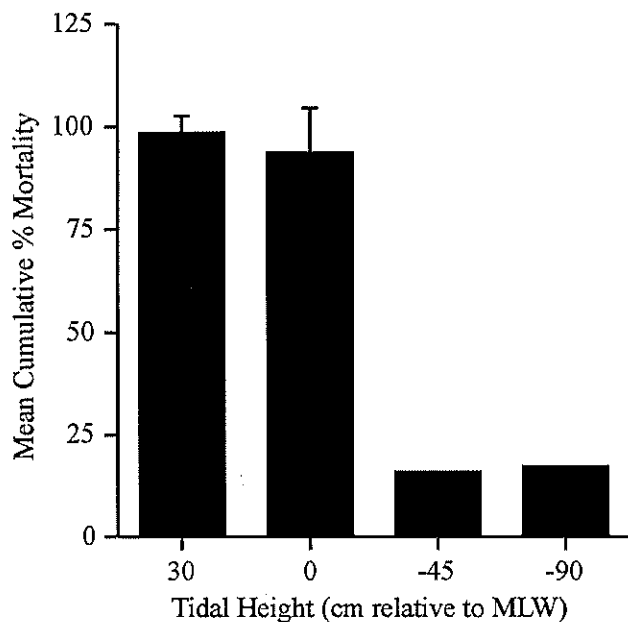


Figure 7. Cumulative percent mortality of juvenile oysters residing at 30 cm above MLW, MLW, 45 cm below MLW, and 90 cm below MLW from November, 1993 -May, 1994. Error bars denote +1 S.E.

and thus are less capable of environmental isolation (Holland and Spencer 1973). In a separate study conducted by the authors over the '94-'95 winter, oysters of a similar age (5 months) and oysters 15 months old residing at MLW experienced winter mortalities between 15 and 20 %. This is evidence that the mortality rates observed over the '93 - '94 winter were exceedingly high.

It should be made clear that the above winter mortalities only reflect oysters at the surface substrate layer, since oysters beneath the reef surface were not measured during the winter months. It was interesting to note, however, that oysters within one cage buried 15 cm beneath the reef surface in the intertidal zone during the '93 -'94 winter (not depicted in the graph), had mortalities of 50 %. This is substantially lower than intertidal mortalities recorded at the surface. Furthermore, visual inspections of "natural set" oysters in underlying intertidal environments revealed higher below surface survivorship. These observations suggest that residence below the reef surface may not only provide refugia from high temperatures and predators during the summer and fall, but may also pro-

vide relief from ice and wind during the winter months.

To recap briefly, settlement/early recruitment of oyster larvae are greatest subtidally, and settlement intensities at the reef surface and 10 cm below the surface are similar. During the summer and fall, subsequent post-settlement survivorship is maximized at MLW; during the winter, mortality of surface dwelling intertidal oysters may be substantial. Survivorship patterns may differ on a smaller spatial scale as well. Submergence 10 cm within the reef provides an important refuge both for intertidal oysters during periods of peak solar exposure (June/July) and for subtidal oysters during periods of intense predation pressure (summer and fall). Furthermore, there is some evidence to suggest that subsurface residence may be beneficial for oysters living in the intertidal zone during the winter months.

In practical terms these results proffer an important lesson: microscale variability should not be ignored when constructing reef systems. Adding merely 1 m of vertical topography onto a constructed reef system so that it may extend marginally out of water at low tide may elevate survivorship substantially, especially if the addition of substrate provides a spatial refuge from intense predation and fouling. This was clearly demonstrated in this study during the summer and fall when mortality rates were lowest at MLW. Unfortunately since mortalities recorded over the winter were a product of unusual circumstances, this study fails to provide a representative comparison between summer, fall, and winter mortalities, which, of course, would be useful in determining whether summer/fall survivorship benefits outweigh mortality losses over the winter. As a result, we cannot provide a definitive answer as to whether building intertidal reefs will maximize survival. Nonetheless, we have shown that tidal elevation does affect settlement and post-settlement survival and that determining the tidal elevation at which recruitment is maximized for a given geographic setting before deciding on a reef elevation is a necessary exercise if survivorship

is to be maximized. Substrate depth also should be considered. The veneer level of shell over a base substrate in reef construction should be thick enough to provide microscale refugia for settlement and survival of early life history stages. Based on the results of this study, the substrate should be at least 10 cm thick and allow for subsurface colonization. Finally, the most important advice we offer to reef builders is to be aware that the issues of settlement and mortality in relation to biological and physical environments are determined by microscale variability rather than larger scale uniformity, and the macroscale patterns observed in the field are the sum of these microscale events.

Acknowledgements

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