12-2004

Evaluating and enhancing the success of oyster reef restoration: The effects of habitat complexity on oyster survival

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FINAL REPORT

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December 31, 2004

Project Summary

We evaluated the progress of several oyster restoration efforts of varying ages in three tidal tributaries of Chesapeake Bay, the Rappahannock, the Piankatank and Great Wicomoco rivers. In 2003 and 2004, we determined the density, biomass and size frequency distribution of oyster populations on the reefs during spring, summer and fall. Recruitment of oysters to the reefs was quantified using standardized substrates deployed and retrieved from the reef surfaces on a weekly or bi-weekly schedule from May through November. The prevalence and intensity of the oyster pathogens *Perkinsus marinus* and *Haplosporidium nelsoni* in oysters on the reefs was determined from samples taken in October 2004 and compared with values taken from another study on the reefs in October 2003. Additionally, the composition and abundance of other epifaunal community constituents associated each of the reefs were enumerated. We characterized the condition of reef base material by measuring the prevalence of present or past damage by boring sponge (*Cliona* spp.) and by measuring individual particle sizes. Finally, large-scale reef attributes such as slope and water depth were quantified. Oyster population data were then related to epifaunal community metrics and substrate condition with correlation analyses.

Our results reveal substantial temporal and spatial variation in oyster populations on the reefs. An important finding of the study was a strong indication that both the unconsolidated shell matrix of the reefs and the oysters on them are subject to physical transport down the slope of the reefs. This appears to contribute to greater than expected number of oysters at the bases of reefs and suggests that future monitoring programs should take care to sample at and around the bases of reefs to assess oyster populations.

The most striking finding of our study was a nearly complete failure of oyster recruitment on most of the reefs during both 2003 and 2004. This failure of recruitment was the primary cause of declining oyster abundances on most of the reefs over the course of the study. Our findings demonstrate, however, that the mean size of oysters increased on all of the reefs over the period, while total biomass of oysters on all of the reefs varied, but did not show any significant declines or increases. Data on oyster size frequencies, pathogen prevalence and intensity, and the abundance of "box" oysters (dead, but still articulated oyster shells) all suggest that the disease was not the primary cause of declining oyster abundance on these reefs. Analyses of substrate condition and epifaunal abundances on the reefs suggest that sufficient clean substrate was available for oyster recruitment. However, frequent sampling for oyster settlement onto reef surface revealed a complete absence of settlement during the early- to mid-summer, the usual time of peak oyster settlement, and in all but one case very low to no recruitment late in the summer. We speculate that, while low brood stock abundances within the tributaries played a role in this recruitment failure, the pattern may largely meteorologically-driven since both years experienced wet, cool springs and early summers.

The failure of oyster populations to increase on the reefs over this period represents a setback to efforts to restore oyster reefs in these tributaries. However, the results of our study caution against a rush to judgment that these declines are all driven by disease mortality and point the importance of integrating monitoring and restoration in an adaptive management mode. Restoration of oyster populations in Chesapeake Bay and its tributaries will require overcoming numerous stresses and population bottlenecks. Approaches that seek simple solutions to this complex issue are unlikely to be successful.

Acknowledgements

This work was supported by grants from the Virginia Coastal Program and the Virginia Oyster Heritage Program to M. Luckenbach. Reefs were constructed from various funding sources under the direction of Dr. James Wesson of the Virginia Marine Resources Commission's Oyster Repletion Program.

We would like to express our thanks to Alan Birch, Sean Fate, Bill Shaw, Joshua Smith, Laurie Sorabella and Ben Wilson for their extensive help in carrying out field sampling, sample processing and data organization. R. Bonniwell, J. Powell and P. Smith also provided field data collection help that was much appreciated. Ryan Carnegie oversaw processing oyster disease samples.

Finally, we thank Pete Hall for allowing us use of Ginnie Point Marina for mooring our boat and as a staging area. This facilitated the implementation of this study immeasurably.

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INTRODUCTION

It is now widely recognized that restoration of oyster reef habitat in mid-Atlantic estuaries is requisite for restoring oyster fisheries and recovering lost ecological services (Burreson et al. 1999). In the Chesapeake Bay region, the Chesapeake Bay Program has adopted a goal of a 10-fold increase in oyster standing stock over the next decade and in Virginia the Oyster Heritage Program is attempting to rehabilitate reef habitats and enhance oyster fisheries. The basic approach of each of these programs is to establish self-sustaining reef sanctuaries that provide valuable ecological functions, such as water filtration and habitat for fish, as well as providing oyster spawning stock to support adjacent harvest areas. While this commitment to restoring these habitats is laudable, there is much that is still unknown about how to properly restore oyster reefs.

In a management context, there are only three things that can be done to restore native oyster reefs: place substrate (usually oyster shell) on the seabed, restrict harvest, and add brood stock. Over the past few years, considerable resources have been allocated to placing substrate on the bottom to promote oyster settlement and growth, and in planting hatchery-reared oysters on some of these reefs. Unfortunately, far too little effort has been allocated to evaluating the success of these efforts and, more importantly, to developing an understanding of how to improve restoration practices. Current monitoring of oysters reefs conducted by the Virginia Marine Resources Commission (VMRC) involves sampling once during the fall of each year using either patent tongs or divers to collect oysters. Oysters in these surveys are classed into one of three categories, *spat, small* and *market*, corresponding roughly to three year-classes and the number of oysters per m^2 recorded. The VMRC conclusion from these samples is that recruitment of oysters is typically enhanced about 10-fold during the first year after shell planting, but that it declines dramatically after that due to degradation of the substrate (Dr. James Wesson, personal communication), leading them to question the efficacy of their restoration efforts.

There are several limitations to the data being used to draw these conclusions. While these monitoring programs are necessary, they fall short of meeting our current needs for several reasons. First, most of these data are being collected from reefs that are only a few years old and we have yet to establish what time course should reasonably be expected for the development of viable reefs. Second, the timing of the sampling (usually Oct. and Nov.) and the categorization of the smallest oysters as "spat" misses the fact that mortality of oysters during the first three months after they settle in the summer (that is, prior to being sampled) may be as high as 98% (Newell et al. 1998). Thus, this sampling glosses over the most critical stage in oyster population dynamics. In drawing the conclusion that oysters are not recruiting to reefs after the first year, this approach fails to provide information on the processes responsible for this or the means to obviate it. As we will describe in the discussion section of this report, when we have evidence about the potential cause(s) of the recruitment failure, we have several options at our disposal to try to enhance recruitment in subsequent years via management decisions.

Finally, it is now abundantly clear that even subtle differences in the size, shape, spatial orientation and complexity of the reef substrate (which we refer to as its *architecture*) can have dramatic effects on recruitment and survival of oysters. Research and monitoring programs need to pay more attention to characterizing the physical condition of the substrate and its relationship to oyster survival. In addition, we need to consider at least two additional monitoring needs. (1) We need to establish *critical point* monitoring that will permit us to employ some adaptive management. For instance, we need to look more closely at settlement rates on reefs to determine if they are limited by new recruits (and thus could benefit from stocking with hatchery stocks) or if early post settlement mortality due to some other factor (such as predation, low dissolved oxygen or algae blooms) is responsible. (2) We need to make explicit comparisons between reefs of differing in location, age, architecture and management techniques in order to evaluate approaches and establish success criteria.

Over the past several years it has become apparent that both large and small scale architecture, such as vertical relief and interstitial space provided by the substrate used for reef bases, can determine whether sufficient numbers of young oysters survive to permit the development of a viable populations (Lenihan and Peterson 1998; Lenihan 1999; Bartol and Mann 1999; Bartol et al. 1999; O'Beirn et al. 2000). For instance, research conducted at Fisherman's Island, Virginia, has shown that, while oysters settle onto reefs constructed out of several different substrates (oyster shell, surf clam shell and coal ash pellets), only the oyster shell bases developed into living oyster reefs with densities reaching nearly 1,500 oysters $\cdot$ m^{-2} (Luckenbach et al. 1998; O'Beirn et al. 2000). Furthermore, we know that the failure of the other substrates to develop viable oyster populations was related to the architecture of the reefs, particularly the interstitial space. (It is also noteworthy that the reefs at Fisherman's Island developed despite high levels of both oyster diseases.)

Despite the success that we have demonstrated in restoring reefs at Fisherman's Island using oyster shell, there is a need to develop alternative substrates for oyster restoration. Oyster shell available for reef restoration is increasingly in short supply. Also, there is the potential that substrates other than shell could reduce competition oysters face from other organisms that burrow into shell.

The Chesapeake Bay Program's Comprehensive Oyster Plan has identified the development of suitable alternative substrates for oyster restoration as a priority area. Considerable research conducted over many years, has demonstrated the suitability of a variety of materials as substrate for oyster settlement (e.g., Haywood et al. 1999); however, little attention has been paid to the details of early post-settlement survival rates on these substrates.

OBJECTIVES

The overall objectives of this study were to evaluate the success of several oyster restoration efforts and to provide ecological information to improve the success of these and future efforts. We sought to better characterize the oyster populations on several "restored" reefs and improve our understanding of the relationships between substrate architecture and the development of viable oyster reefs. Specific objectives for this study were to:

1. Characterize the oyster populations on several "restored" reefs in an effort to evaluate their success;
2. Describe the condition of the reef base material on several reefs of differing ages and examine the relationship between the condition of the material and recruitment of new oysters;
3. Evaluate the effectiveness of several alternative substrates for reef restoration, especially as they relate to enhancing the recruitment and early survival of oysters; and
4. Relate recruitment rates and survival rates for newly-recruited oysters to habitat complexity and reef architecture.

STUDY AREA/REEFS

This research project was conducted on six man-made reefs of varying ages in three Virginia tributaries of the Chesapeake Bay, USA (Table 1 & Figure 1). Latitude and longitude

Table 1. Reefs of varying ages in three Virginia tributaries of the Chesapeake Bay, USA, included in this study (see Appendix I and Figure 1 for specific geographic information).

Tributary	Reef	Year constructed
Great Wicomico River	Crane's Creek Reef (CC)	1998
	Shell Bar Reef (SB)	1996
Piankatank River	Burton's Point Reef (BP)	1995
	Palace Bar Reef (PB)	1993
Rappahannock River	Drumming Ground Reef (DG)	2000
	Parrot Rock Reef (PR)	2000

coordinates for each site are given in Appendix I. Historically, this region was considered a highly productive oyster area with extensive natural reefs (Hargis 1999). The area is a mix of state-owned and privately leased bottom that has previously supported a substantial oyster industry, based both upon harvesting wild oysters and transplanting seed oysters to private leases. Specific sites chosen for the study were deemed to have been historically highly productive and, therefore, important to overall oyster reef restoration in the region.

The rivers in this study are generally mesohaline tributaries with a 10-year average mid-water column salinity of 19 psu, 16 psu and 16 psu for the Great Wicomico, Rappahannock and Piankatank Rivers, respectively, in the vicinity of the study reefs. Water temperature and salinity data are available from the Chesapeake Bay Program's fixed monitoring stations for each tributary for the study period (http:\\www. chesapeakebay.net/data/index.htm). It was notable that higher than average rainfall during the 2003-2004 seasons led to relatively low salinities in all 3 tributaries (Figure 2).

Figure 1. Study area map of lower Chesapeake Bay, USA. Insets are specific locations of individual reefs for each tributary. See Appendix I for exact reef coordinates and Table 1 for reef name abbreviations.

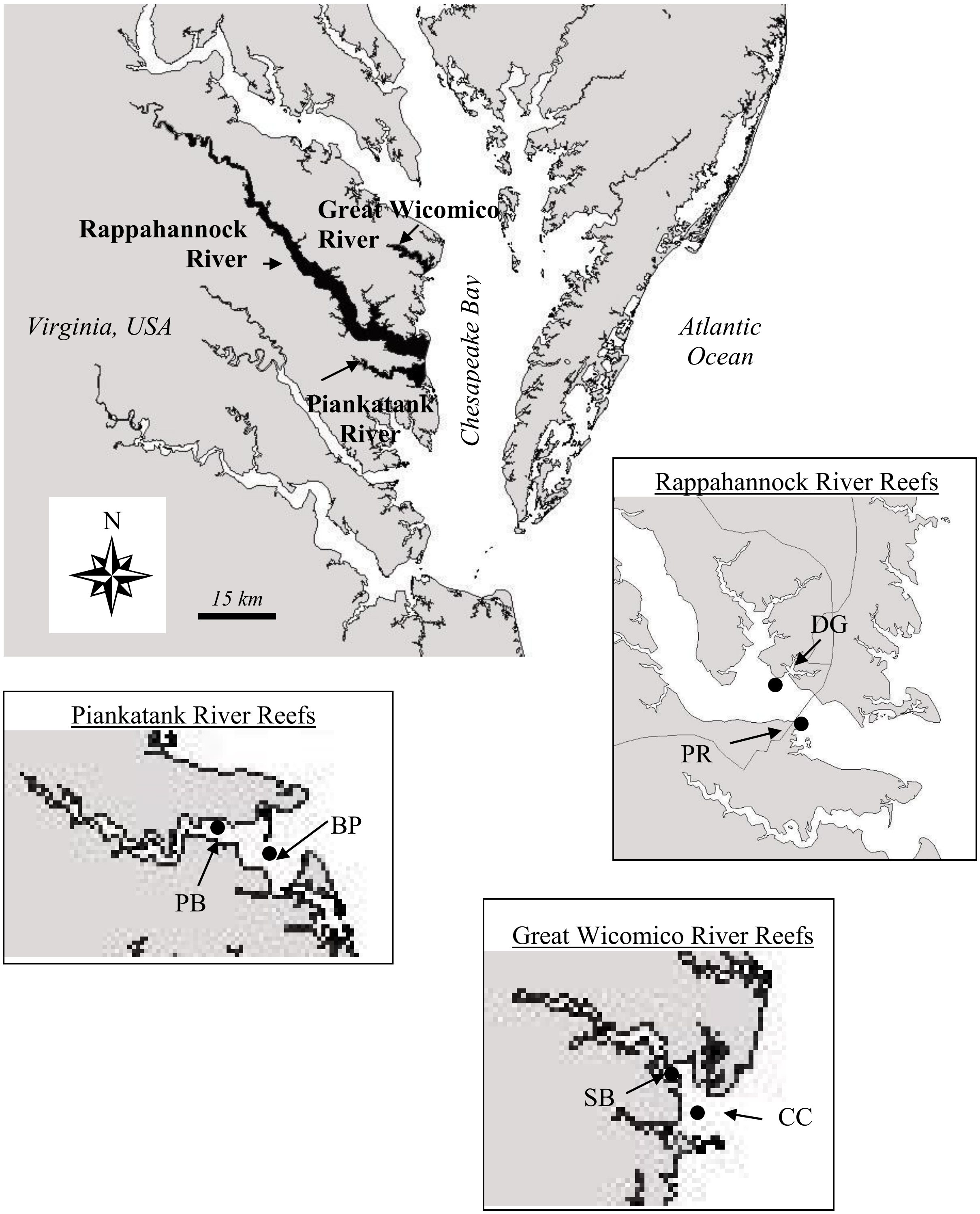
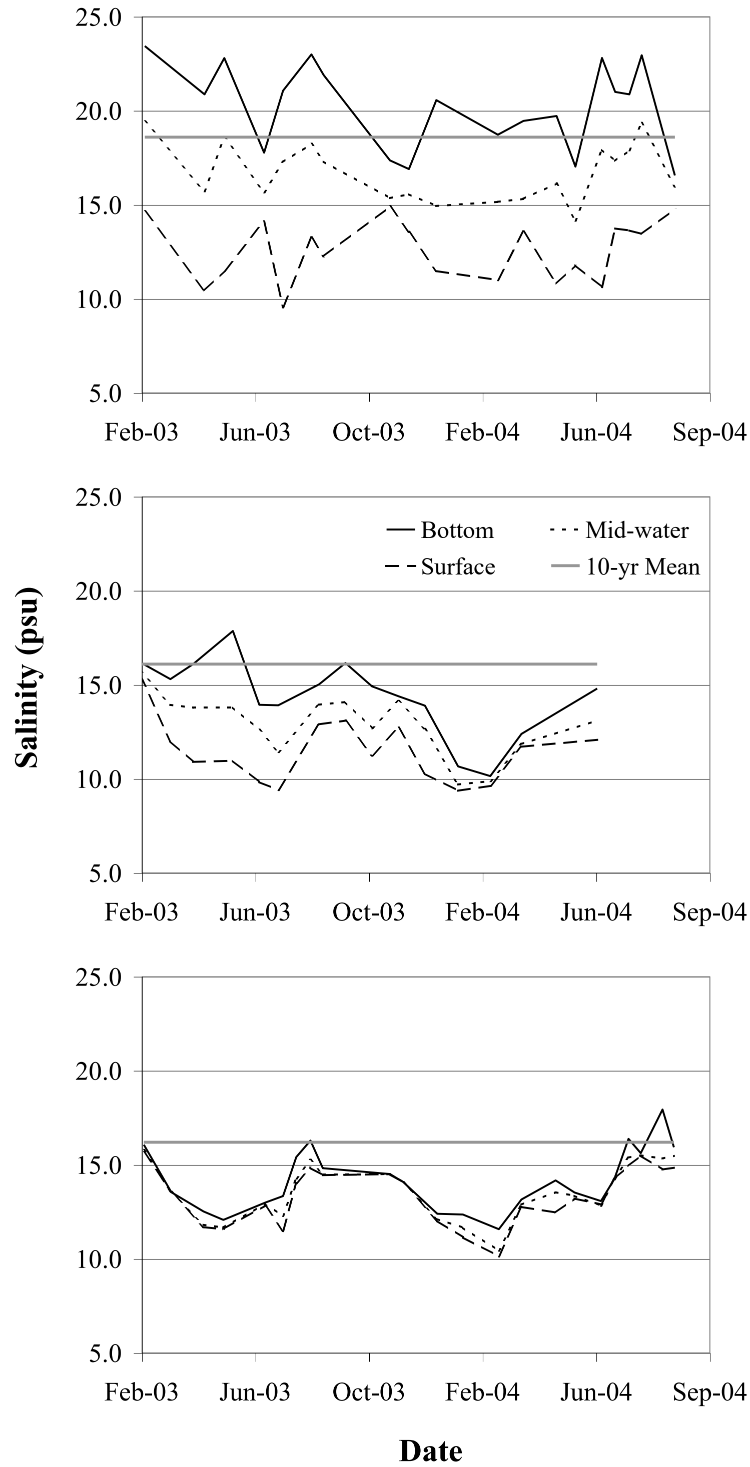


Figure 2. Salinity (psu) for bottom, mid-water and surface depths at representative monitoring stations for the three tributaries in this study. Mean 10-year mid-water column salinity is plotted as a gray bar for reference. Data were downloaded from the Chesapeake Bay Program website (http://www.chesapeakebay.net/data/index.htm) and correspond to monitoring stations CB 5.4, LE 3.4 and LE 5.7 for the Great Wicomico, Rappahannock and Piankatank Rivers, respectively.

(A) ***Great Wicomico River***

(B) ***Rappahannock River***

(C) ***Piankatank River***



Reef Design and Construction

The Virginia Marine Resources Commission constructed the reefs included in this study from 1993-2000. High relief reef bases were constructed by placing shell piles (Figure 3) in arrays (Figure 4). Core material for individual mounds was comprised of surf clam (*Spisula solidissima*) shell that was capped off with a veneer (~15 – 20 cm) of clean oyster shell. Overall, this created 'upside-down egg carton' shaped sub-tidal reefs. However, in some of the shallower and older reefs, mounds have washed together in places to create more contiguous reef architecture. Reefs ranged in size from approximately 4,000 m^2 to 6,000 m^2. Appendix II contains aerial photographs and schematics for each reef. Other reef-specific descriptors will be discussed in the results and discussion sections.

Figure 3. Generalized side view of an individual shell mound.

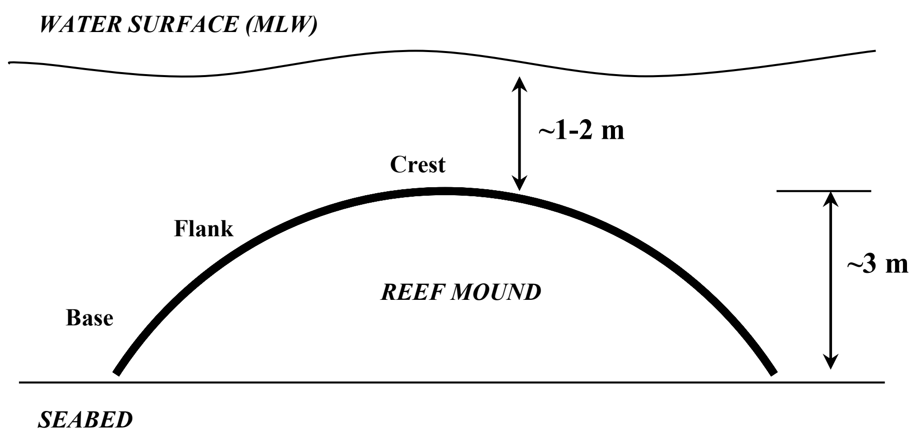
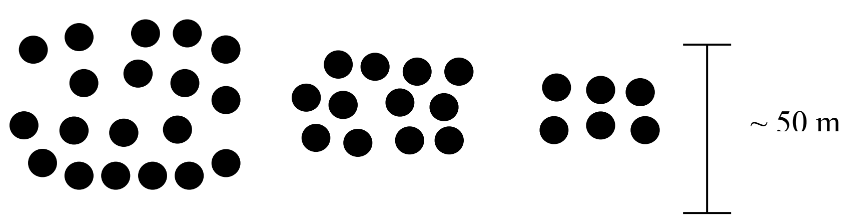


Figure 4. Generalized aerial footprint of a study reef. Each circle represents a mound approximately 10 m diameter as shown in Figure 3. Appendix II contains aerial photographs and schematics for each specific reef.

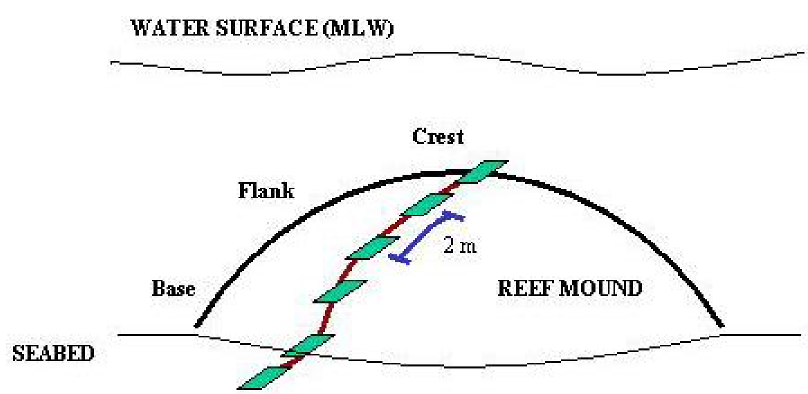


METHODS

Reef Monitoring

Diver Collected Quadrate Samples – Quadrate samples of reef material were collected by divers to describe epifauna (including oysters) and characterize reef substrate. Samples were collected haphazardly from different mounds within reefs during spring, summer and fall of 2003 and 2004. All reef material in a 25 cm x 25 cm frame was excavated to a depth of 10 cm. Samples included the crest and flank portions of reefs in 2003 and crest, flank and base portions of reefs in 2004 (Figure 3). Additionally, quadrates were collected along 3 replicate transects every two m from reef crest to seabed on two reefs during summer and fall 2004 to further elucidate elevational differences in oyster abundances on reef mounds (Figure 5). Appendix III reports the specific dates and numbers of replicates for these quadrate samples.

Figure 5. Diagram of transect samples from reef mound crest to the seabed-reef interface.



All live oysters and the articulated shells of dead oysters (henceforth referred to as "boxes" or "box oysters") were counted and shell heights (longest hinge-lip distance) measured to the nearest 0.1 mm. During spring, summer and fall of 2004, a sub-sample of 339 of these oysters covering the full size range encountered during the study was selected and processed to determine ash-free dry tissue weight (AFDW). Individuals were dried to a constant weight at 90°C and ashed at 538 °C for 5 hours to determine AFDW. A best-fit power function was then computed relating shell height to AFDW. This relationship was then used to compute biomass for all oysters sampled.

Other attached epifauna (e.g. barnacles, sea squirts and boring sponge) were identified and enumerated by either counting individuals or estimating % cover, whichever was appropriate to specific taxonomic groups (see Table 2 for details).

Table 2. Metrics used to quantify abundance of epi-benthic organisms of various taxonomic groups enumerated in this study.

Taxonomic Group	#/m^2	% Cover[a]
Bivalves	X	
Tunicates	X	
Anemones	X	
Gastropods	X	
Flatworms	X	
Barnacles		X
Encrusting Bryozoans		X
Calcareous Tube Worms[b]		X
Sponges		X
Macroalgae		X
Hydroids		X

[a] % cover estimated subjectively: <1%; 1-10 % in increments of 1%; 10-100% in increments of 5%
[b] % cover of tubes estimated. These are constructed by several polychaete species

Additionally, 25 oysters from each reef were collected during early October 2004 to test for the prevalence and intensity of two important oyster diseases. *Perkinsus marinus* infections were diagnosed with Ray's Thioglycollate medium assays (Ray 1952). *Haplosporidium nelsoni* infections were diagnosed using standard histological techniques

(Burreson et al. 1988). The VIMS Shellfish Pathology Laboratory performed all disease diagnoses. Comparable data for four of the six reefs from 2003 that were collected during other projects are also reported for comparisons to 2004 disease data.

Sub-samples of reef material were gathered from quadrate samples to characterize some physical parameters of individual reef particles. The type of individual particles (i.e. oyster, clam or other) was recorded as were the number of particles showing evidence of current or previous boring sponge (*Cliona* spp.) presence, which leads to shell degradation. Boring sponge damage is evident as perforations in the shell. Finally, the entire sub-sample was digitally imaged (Figure 6) and Image Pro Plus computer software was utilized to determine the one-sided surface area of individual particles to the nearest mm^2.

Oyster Settlement – Replicate settlement collectors consisting of arrays of 4" x 4" ceramic tiles (Figure 7) were deployed within 10 cm of reef surfaces on a fortnightly or weekly schedule throughout the summer of both years (see Appendix IV for details on deployment and retrieval dates and replicates). Gear was deployed at or near reef crests and bases within

Figure 6. Examples of reef particle samples analyzed for shell type, *Cliona* spp. evidence and surface area (mm^2). Photos show examples of (A) large oyster shell particles and (B) predominantly smaller clam shell particles. The scale bar in each image is 150 mm long.

(A) **(B)**

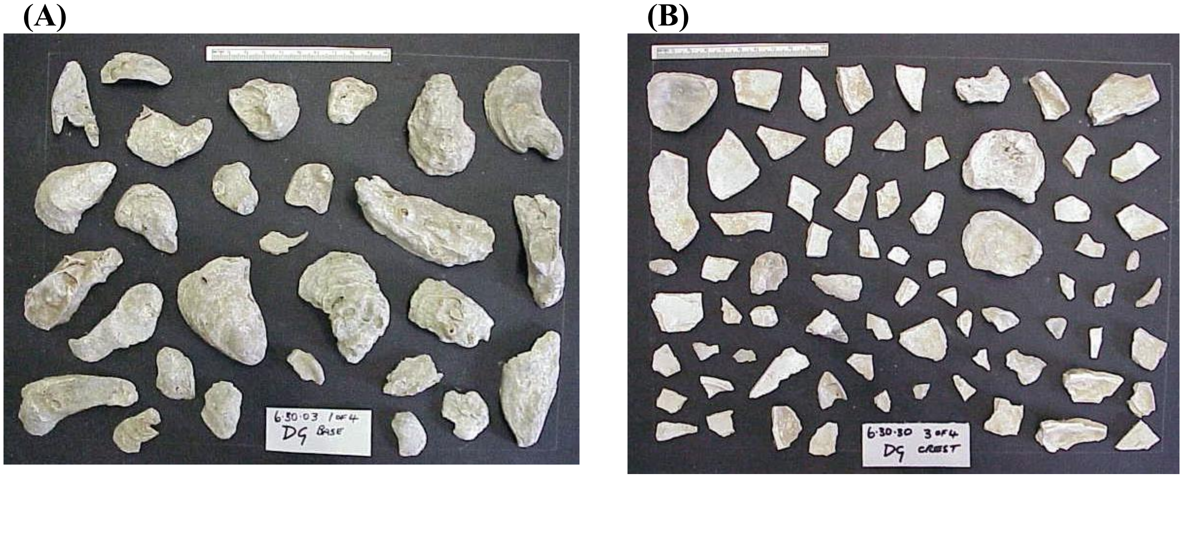
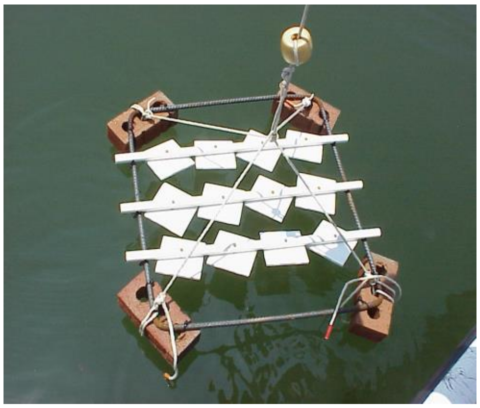


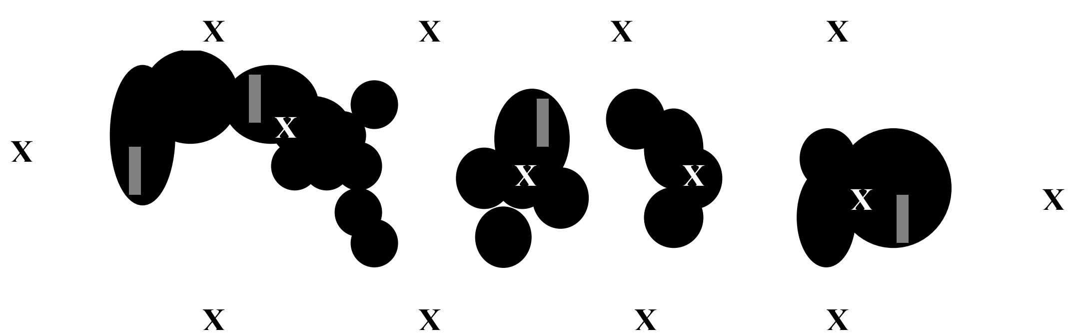
Figure 7. Array of ceramic tiles used to assay oyster settlement on reefs.



each reef. The numbers of oysters settling on tiles were examined under a microscope in the laboratory. We have previously used this technique in other another study on oyster reefs in the Rappahannock River and find that it provides a reliable estimate of the rates of recruitment of oysters to the reefs (Luckenbach and Ross 2003).

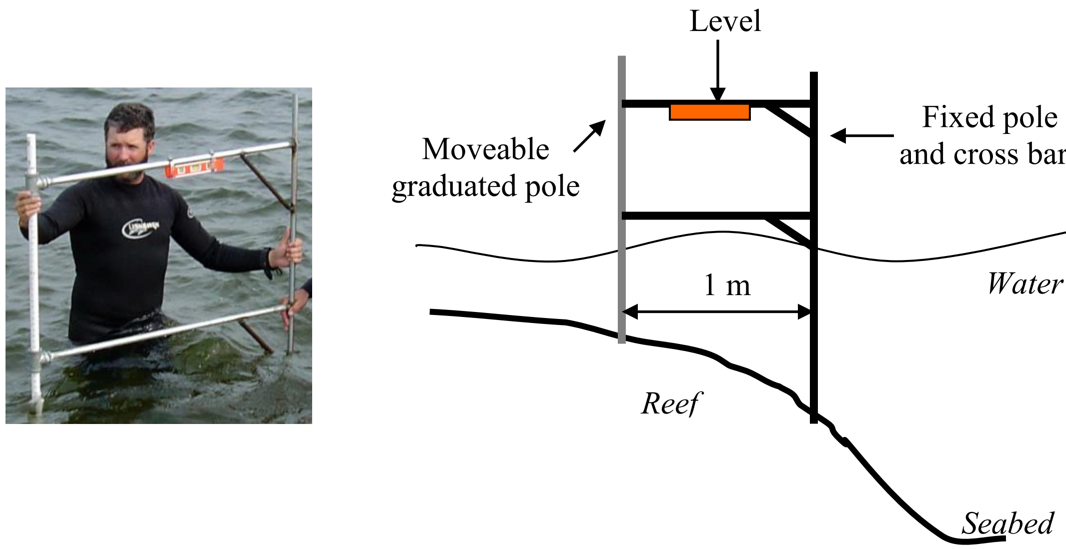
Large-scale Reef Attributes – During 2004 we characterized several larger scale attributes of all six reefs: seabed depth around reefs, reef crest depths and % slope of reef mounds. Seabed and reef crest bathymetry (10 and six soundings per reef, respectively; Figure 8) were measured using a transom-mounted Garmin depth sounder (150 watts, 200 mHz). Depth calibrations were made using a graduated staff and related to sounder readings. Depths were standardized to mean lower low water (MLLW) based on the time of data collection and published tide predictions at nearby stations.

Figure 8. Generalized locations of seabed (X) and crest (white X) soundings and slope measurements (grays bars) using schematic of one reef as an example.



Percent slope was measured as *rise/run*100*, with a resolution of one meter (Figure 9). Measurements were made near the crest, on the flank and near the base of four different locations on each reef (i.e. 12 measurements per reef).

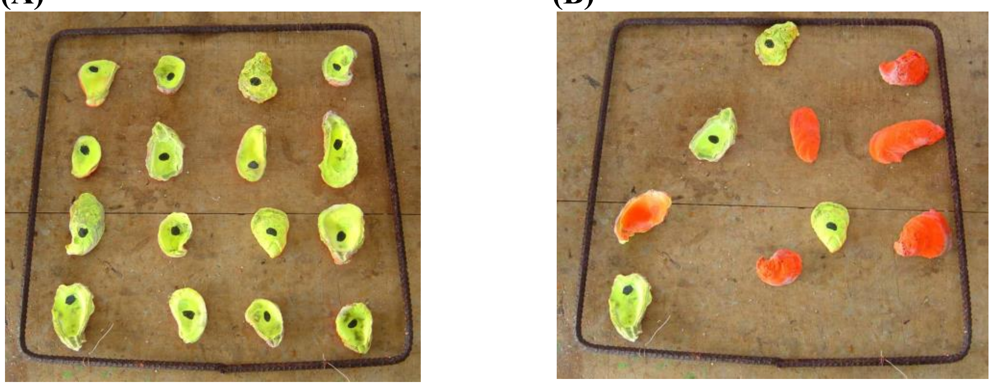
Figure 9. Device used to measure the slope of reef mounds over a distance of one meter. A calibrated moveable graduated pole was used to measure rise to the nearest 2 cm over a fixed run of 1 m.



Shell Movement Experiment – Our observations suggested that oyster abundances potentially differed along a gradient from reef crest to base. Furthermore, anecdotal evidence showed that these differences may have been related to physical forces acting on the unconsolidated reef veneers. Therefore, we conducted a small-scale experiment to examine movement of oyster shells in the reef veneer during fall 2004. Representative oyster shells were painted fluorescent yellow on one side and fluorescent orange on the other (Figure 10). Arrays consisting of 16 of these shells were deployed, yellow side up, at a crest and flank location on each reef by divers on Sept. 15, 2005 and retrieved on Oct. 10, 2004. The number of shells remaining within the quadrate and the number with orange side up were recorded to estimate shell movement either linearly or by flipping in place (however, there was no way of knowing if a shell flipped and then flipped back to the yellow side at some point during the deployment). Additionally, the immediate vicinity (within two m) of the deployment site was then searched and the distance to any marked shells was measured.

Figure 10. Painted shell arrays (A) as deployed (minus the frame) and (B) example of remains after 20 days on a reef (minus frame).

(A) **(B)**



Substrate Experiment

One-hundred and sixty baskets (45 x 45 x 25 cm) containing one of a variety of substrates (Table 3 & Figure 11) currently or potentially being used for reef restoration in the Chesapeake Bay were deployed near the Palace Bar reef in the Piankatank River during the spring 2003 (Figures 12 & 13). Interstitial volume was determined for each unit via water displacement prior to deployment. First, the potential volume (Vol_{pot}) of a cage of substrate was measured as: cage width x cage depth x height of material in a cage (the latter term simply allows for minor corrections in height to account for some materials reaching slightly above or below the top of the cages). Second, cages with substrate were submersed in a large tank of water and the water displaced by the unit (i.e. cage and material combined) was captured and measured ($Vol_{sub+cage}$). The total interstitial volume was then calculated by:

$$\textit{Total Interstitial Volume} = Vol_{pot} - Vol_{sub+cage}$$

Replicate baskets were to be retrieved at intervals between summer 2003 and fall 2004 and the numbers and sizes of oysters determined. Image analysis was to be used to characterize the surface complexity (roughness and fractal dimension) of the various substrata and to describe the size and configuration of interstitial space within the treatments. Oyster recruitment, growth and survival were to be related to the substrate type, the size of the material and various measures of habitat complexity. However, oyster recruitment was extremely low during both 2003 and 2004 severely limiting our ability to properly complete this experiment. The reasons and impacts of this recruitment failure on the alternative substrate portion of this study will be expanded upon in the results and discussion sections of this report.

Table 3. Alternative substrate types and sizes deployed near the Palace Bar reef in the Piankatank River.

Material	Size Classification	Dimension Limits (cm^2)[a]	% Interstitial Volume[b]
Oyster Shell	-	-	60.8
Surf Clam (*Spisula* sp.) Shell	-	-	54.0
Recycled Concrete	-	20-81	36.3
Cinder Block	-	188-360	57.4
Limestone Marl	Large	460-686	54.5
	Small	188-360	50.9
Granite	Large	310-574	33.5
	Small	80-202	37.1

[a] Dimension limits refer to generalized rectangles representing the upper and lower bounds of projected 2-dimensional areas of the particles.
[b] Mean interstital volume for an entire cage. See Figure 33 in the results section for measures of variance and more specifics.

Figure 11. Several examples of alternate substrates deployed in the Piankatank River (see table 3 for complete details on all materials): (A) Large granite, (B) small granite and (C) oyster shell. The black bar in each image is approximately 45 cm long.

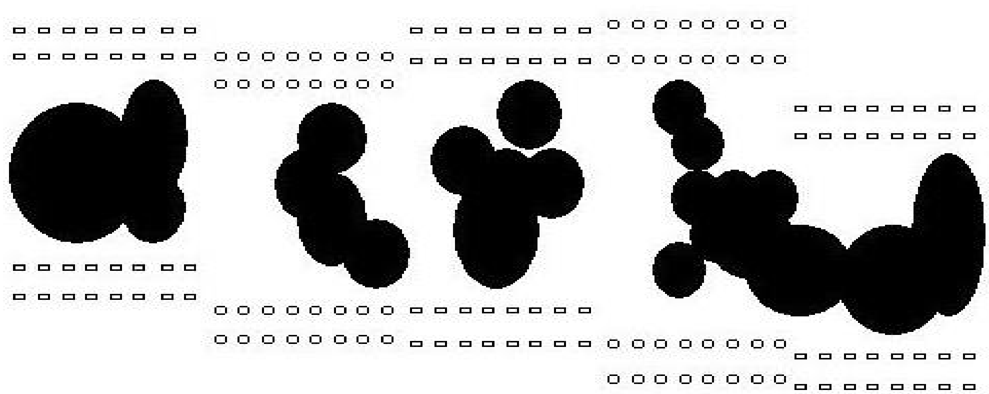
(A)

(B)

(C)

Figure 12. Deploying one of 160 cages of reef substrate. Cages weighed between 150 and 200 lbs. (70-90 kg) at deployment.

Figure 13. Generalized schematic of alternative substrate cage deployment in a blocked design around the Palace Bar Reef in the Piankatank River. Squares and circles represent individual cages.



Statistical Analysis

Our experimental sampling designs were established to permit analyses via ANOVA; however, much of the data exhibited either non-normal distributions or heteroscedasticity. Therefore, we chose to perform most analyses on ranked data following standard non-parametric techniques, except where noted otherwise in the results section. Kruskal-Wallis tests were used for one-way comparisons and Friedman's method was used for analyzing differences in two-way models (e.g. *sample date* and *reef*; Sokal and Rohlf, 1997). Significant main effects elucidated by Friedman's method were subsequently analyzed separately using Kruskal-Wallis tests. Where appropriate, Tukey's multiple comparisons were used to determine specific differences (Sokal and Rohlf, 1997). All percent data were arcsine transformed prior to analysis (Sokal and Rohlf, 1997). Pearson product-moment correlation coefficients were used to relate oyster population parameters to other variables (e.g. barnacle % cover, particle size or reef slope). The null hypotheses that these correlation coefficients did not differ from zero were tested using t-tests (Sokal and Rohlf, 1997). All statistical tests were run using SAS™.

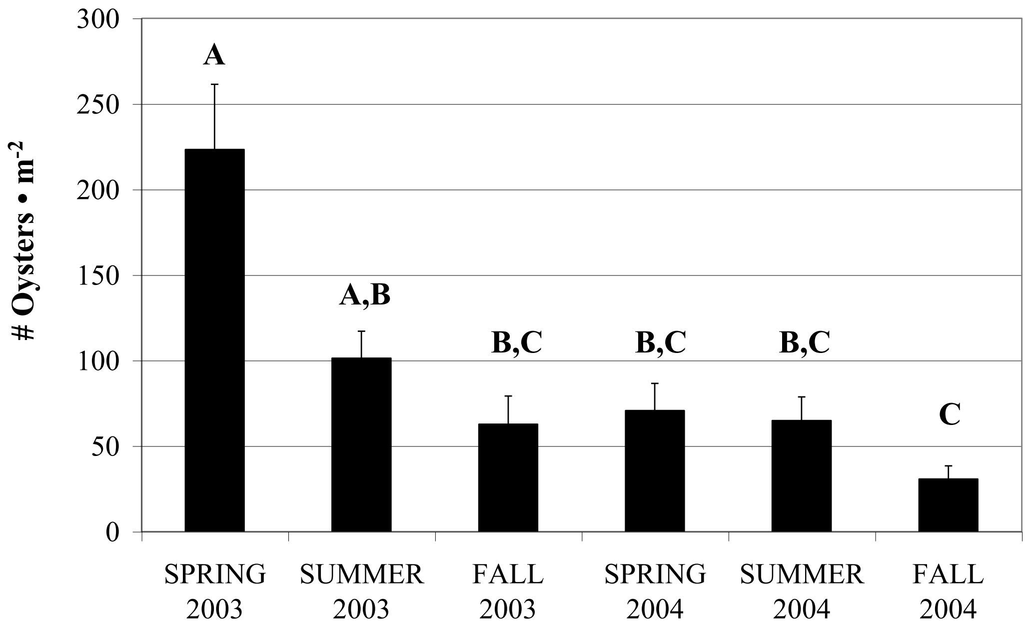
RESULTS

Oyster Abundance and Biomass

Abundance -- Overall, 180 quadrate samples were collected during the two years of this study. Appendix V contains summary abundance data for individual reefs sampled during each season throughout the study. Sample sizes for each reef during each date were four and six quadrates for 2003 and 2004, respectively.

Data pooled for all reefs on the density of live oysters ($\# \bullet m^{-2}$) over the course of this project indicate a significant general downward trend ($p<0.0001$), declining from 223 (SE=38) at the beginning of the study in spring 2003 to a low of 31 (SE=8) by the end of the study in fall 2004 (Figure 14). Overall mean density during the entire study ranged from 108 (SE=16) oysters • m^{-2} at Shell Bar reef to 55 (SE=12) oysters • m^{-2} at Crane's Creek reef.

Figure 14. Mean (+SE) live oyster densuty (# • m^{-2}) over time (data pooled for all reefs). Means with different letters are significantly different (P<0.05).



Significant *sample date* and *reef* effects were observed for live and "box" oyster densities (Appendix VI). Although no significant differences (p>0.05) were observed for live oyster abundance between reefs when analyzed for individual seasons, several were close to being significant (summer 2003, p=0.0566; fall 2003, p=0.0821; and summer 2004, p=0.0749). However, no consistent pattern developed between reefs as the study progressed (Table 4). The abundance of "box" oysters exhibited significant differences between reefs for summer 2003 and fall 2004 only (p=0.0193 and p=0.0100, respectively). Although no dominant patterns were observed, Shell Bar and Crane's Creek reefs had the highest abundance of "boxes" during these two periods (Table 4).

Significant differences were observed for live oyster abundance on individual reefs

Table 4. Comparison between reefs[a] for each sample date for (A) # live oysters • m^{-2}, (B) # "box" oysters • m^{-2} and (C) biomass (g) of live oysters • m^{-2}. Reefs means (SE) are listed in descending order for each date. Where significant differences were observed, means with different letters were significantly different within each individual sample date (n=4 for each reef/date for 2003 and n=6 for each reef/date for 2004).

(A)

Spring 2003^{NS}		Summer 2003 ^{NS}		Fall 2003 ^{NS}		Spring 2004 ^{NS}		Summer 2004 ^{NS}		Fall 2004 ^{NS}	
PB	360 (123)	PB	152 (43)	BP	104 (44)	DG	125 (69)	SB	104 (23)	SB	72 (31)
PR	332 (74)	PR	128 (40)	SB	100 (40)	PB	107 (36)	PR	101 (43)	PR	37 (17)
SB	228 (59)	CC	116 (18)	DG	92 (56)	SB	80 (30)	PB	96 (49)	CC	29 (20)
BP	188 (119)	BP	112 (33)	PR	44 (44)	PR	64 (40)	DG	35 (25)	DG	24 (14)
CC	128 (49)	SB	100 (16)	CC	36 (31)	CC	27 (13)	CC	32 (26)	PB	19 (10)
DG	104 (88)	DG	0 (0)	PB	0 (0)	BP	21 (14)	BP	21 (18)	BP	3 (3)

(B)

Spring 2003^{NS}		Summer 2003*		Fall 2003 ^{NS}		Spring 2004 ^{NS}		Summer 2004 ^{NS}		Fall 2004*	
BP	40 (8)	SB	60 (27)^{A}	DG	36 (21)	DG	56 (33)	PR	21 (13)	SB	40 (11)^{A}
SB	32 (17)	CC	40 (15)^{A,B}	BP	32 (9)	SB	24 (14)	PB	19 (13)	PR	19 (12)^{A,B}
CC	28 (10)	PB	40 (25)^{A,B}	SB	28 (18)	PB	13 (6)	DG	16 (10)	DG	16 (16)^{A,B}
PB	12 (8)	PR	16 (7)^{A,B}	CC	20 (15)	CC	8 (8)	SB	16 (7)	CC	11 (5)^{A,B}
PR	12 (12)	BP	8 (5)^{A,B}	PB	0 (0)	PR	27 (13)	BP	3 (3)	BP	0 (0)^{B}
DG	4 (4)	DG	0 (0)^{B}	PR	0 (0)	BP	8 (5)	CC	0 (0)	PB	0 (0)^{B}

(C)

Spring 2003^{NS}		Summer 2003 ^{NS}		Fall 2003 ^{NS}		Spring 2004 ^{NS}		Summer 2004 ^{NS}		Fall 2004*	
SB	159.6 (132.6)	PB	72.7 (40.8)	BP	40.1 (10.3)	PB	81.8 (45.3)	PR	98.8 (62.3)	CC	82.6 (36.4)^{A}
PB	107.3 (42.7)	SB	72.4 (56.5)	DG	36.9 (36.9)	DG	70.4 (63.4)	PB	78.9 (36.4)	SB	57.3 (22.8)^{A,B}
PR	71.9 (4.1)	PR	56.2 (19.8)	SB	31.8 (6.9)	SB	51.9 (30.5)	SB	75.7 (22.4)	PR	29.5 (11.1) ^{A,B}
BP	41.1 (17.3)	CC	47.6 (14.0)	PR	29.9 (29.9)	PR	39.2 (25.8)	DG	21.0 (17.0)	DG	13.1 (13.1) ^{A,B}
CC	30.4 (15.8)	BP	44.7 (1.3)	CC	17.1 (4.9)	BP	13.7 (13.7)	CC	13.6 (9.6)	PB	11.5 (8.1) ^{A,B}
DG	20.5 (17.3)	DG	0.0 (0.0)	PB	0.0 (0.0)	CC	13.6 (9.8)	BP	10.6 (10.1)	BP	0.8 (0.8)^{B}

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock
^{NS} indicates 'No Significant Difference' between reefs
* indicates means were significantly different, p<0.05, between reefs for this sample date

over time at Crane's Creek ($p=0.0306$), Burton's Point ($p=0.0004$), Palace Bar ($p=0.0020$) and Parrot's Rock ($p=0.0222$), but not at Shell Bar and Drumming Ground reefs ($P>0.05$). Although substantial variability was present, a definite downward trend was seen at all reefs from beginning to end of the study (Figure 15). While the "box" oysters exhibited significant differences over time at Crane's Creek and Burton's Point reefs only ($p=0.0176$ and $p<0.0001$, respectively), no consistent pattern emerged at all reefs (Figure 16). "Box" abundance appeared to increase, decrease, remain stable or vary considerably, depending on the reef.

Biomass -- We computed a regression between shell height and ash-free dry weight on a sub-sample of 339 oysters (Figure 17) to estimate the dry tissue biomass (henceforth referred to as "biomass") of all oysters collected during the study in quadrate samples (Appendix VII). The best-fit power function curve fit to the data yielded the equation **BIOMASS (mg) = 0.05 • SHELL HEIGHT$^{2.338}$** which had a 0.693 R^2-value. This equation was subsequently used to calculate biomass for every oyster collected during the study.

Data pooled for all reefs on the biomass of live oysters ($g \bullet m^{-2}$) over the course of this project indicate no significant difference ($p=0.0913$) between sample dates. Overall mean biomass during the entire study ranged from 72 (SE=19) $g \bullet m^{-2}$ at Shell Bar reef to 21 (SE=6) $g \bullet m^{-2}$ at Burton's Point reef.

Significant differences in oyster biomass per area were observed across reefs when analyzed over the entire study period (Appendix VI). However, when analyzed within individual seasons, only during fall 2004 was a significant difference between reefs observed ($p=0.0245$; Table 4). No significant differences ($P>0.05$) were observed for live oyster biomass on individual reefs over time for individual reefs (Figure 18).

Figure 15. Mean (+SE) live oyster abundance (# • m^{-2}) over time for individual reefs in (A) Great Wicomico River, (B) Piankatank River and (C) Rappahannock River. Within each graph, NS indicates no significant differences between dates, while means with different letters are significantly different (P<0.05). For each individual, reef n=4 and n=6 for dates in 2003 and 2004, respectively.

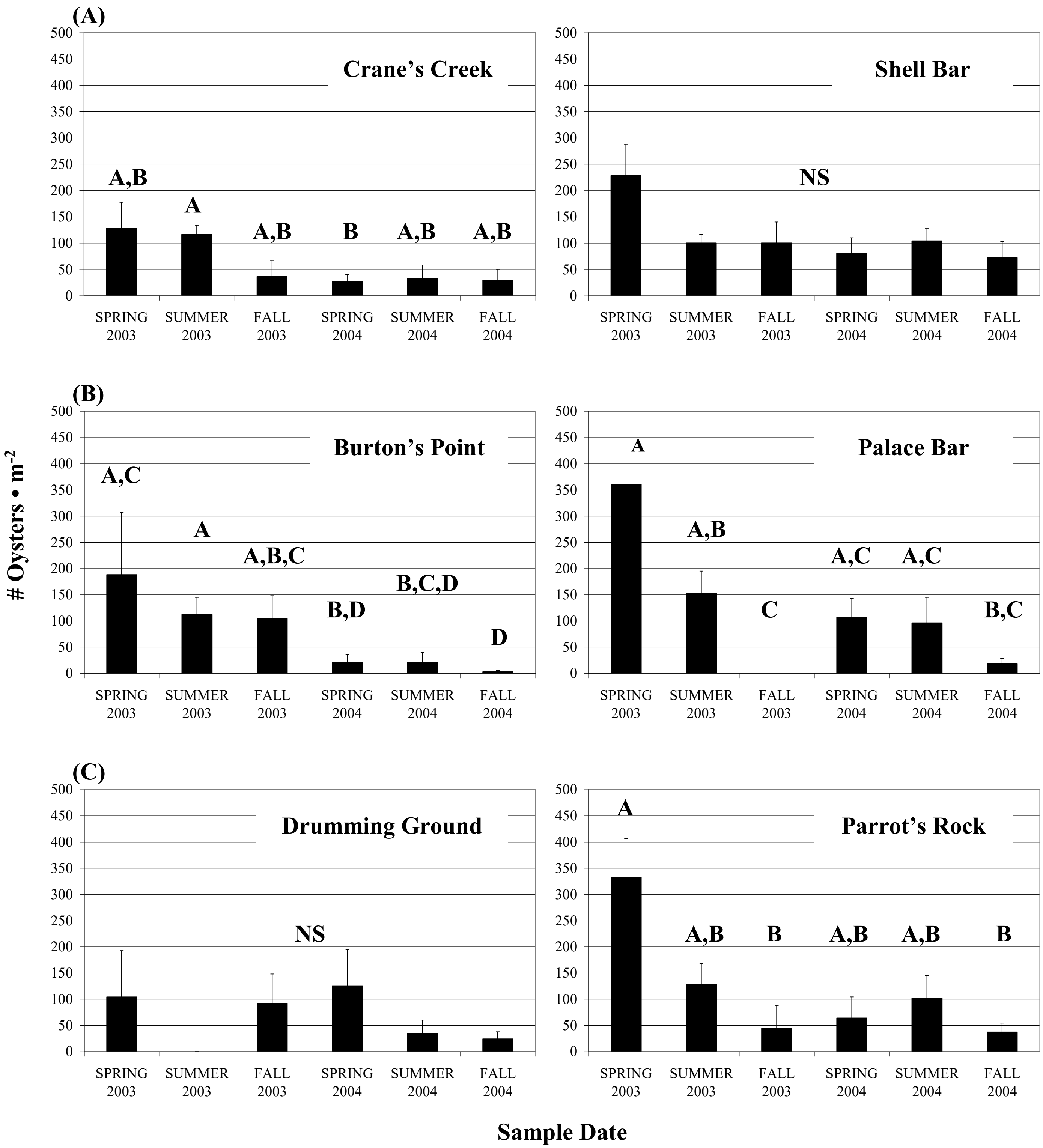


Figure 16. Mean (+SE) "box" oyster abundance (# • m^{-2}) over time for individual reefs in (A) Great Wicomico River, (B) Piankatank River and (C) Rappahannock River. Within each graph, NS indicates no significant differences between dates, while means with different letters are significantly different (P<0.05). For each individual reef, n=4 and n=6 for dates in 2003 and 2004, respectively.

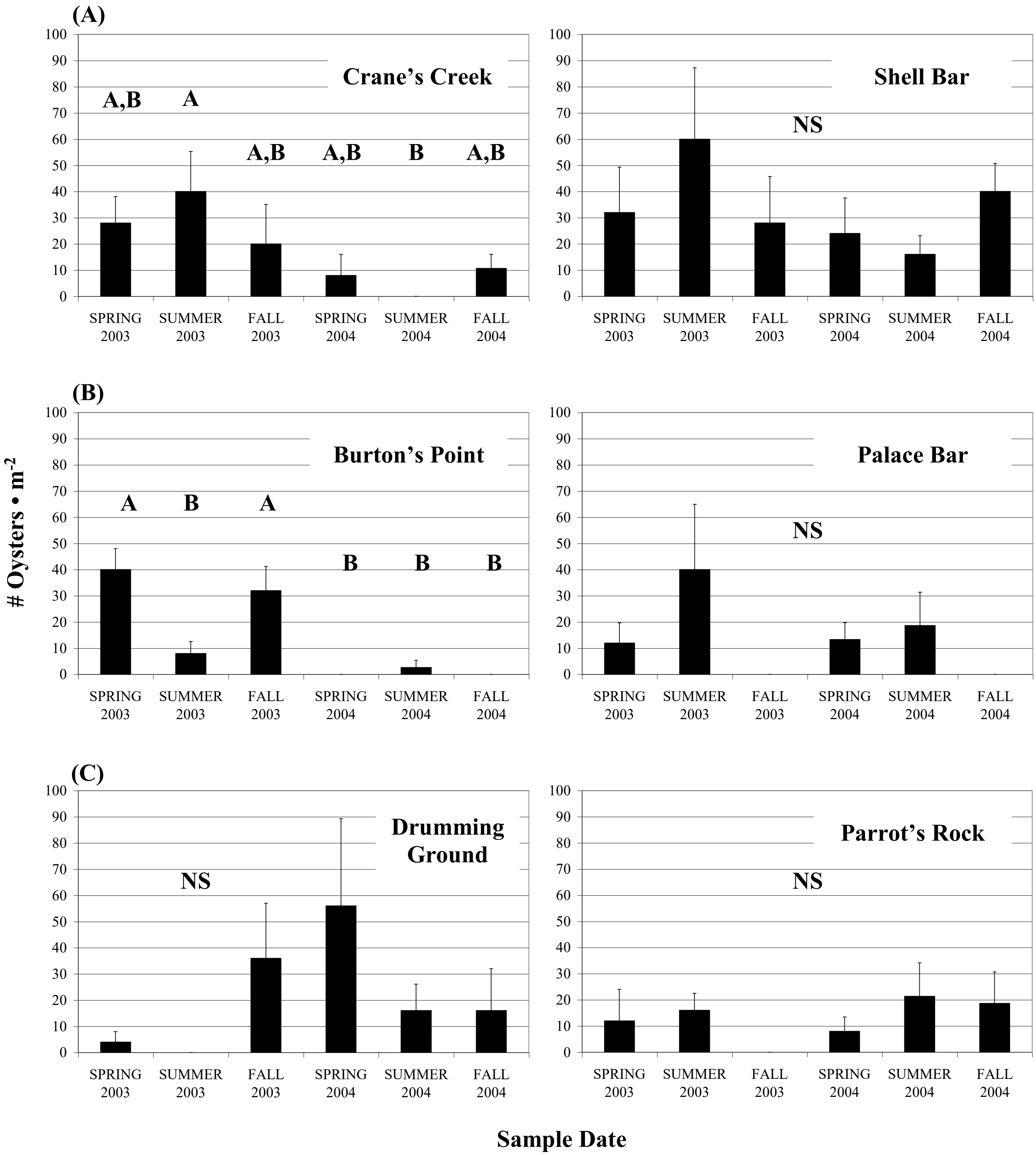
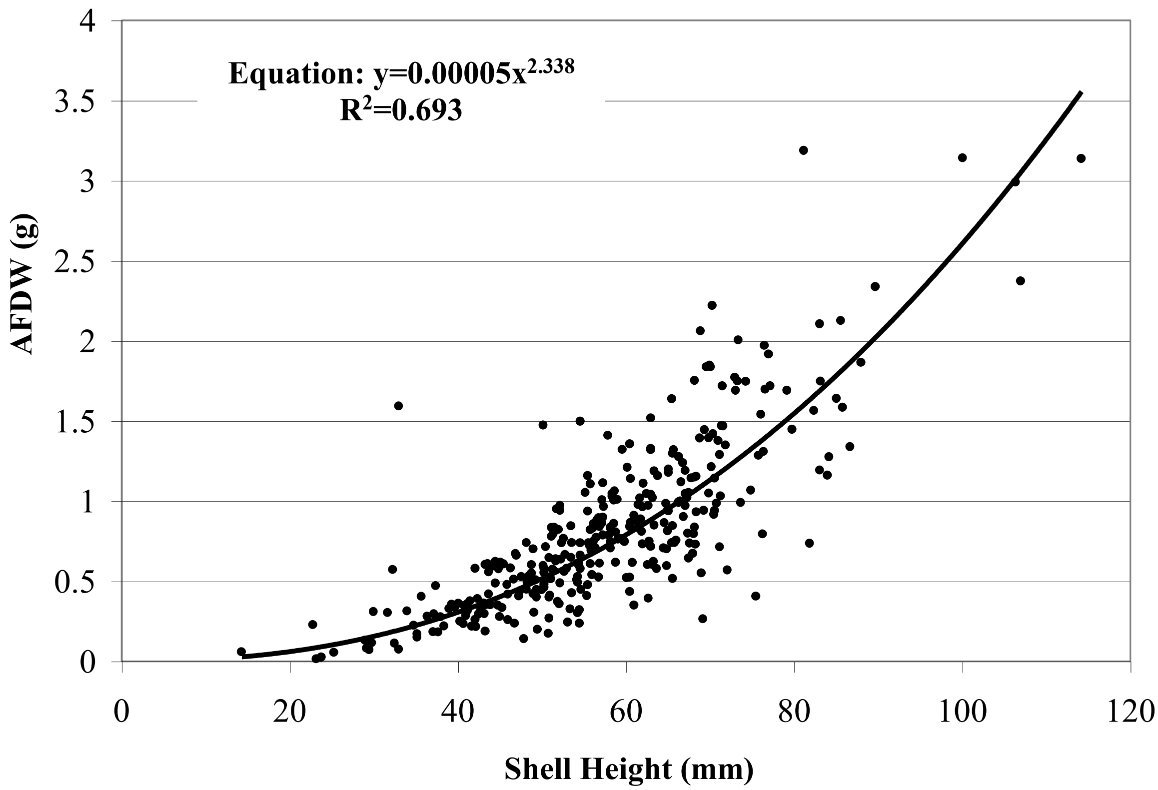


Figure 17. Regression between oyster shell height and ash-free dry weight of tissue (AFDW). Curve is a best-fit power function.



Oyster Size

All 992 of the live and 215 of the "box" oysters collected in quadrate samples during the two years of this study were measured. Appendix VII & VIII contain summary size data (shell height and individual biomass, respectively) for reefs sampled throughout the study. The number of quadrate samples for each reef during each date was four and six for 2003 and 2004, respectively. Multiple year classes of live oysters, based on shell height, appear to be evident at most reefs (Figures 19-24). This was most evident at Shell Bar reef (Figure 20), where substantial plantings of adult oysters occurred in 2003 and 2004.

Figure 18. Mean (+SE) live oyster dry tissue biomass (g • m^{-2}) over time for individual reefs in (A) Great Wicomico River, (B) Piankatank River and (C) Rappahannock River. Within each graph, NS indicates no significant differences between dates, while means with different letters are significantly different (P<0.05). For each individual reef, n=4 and n=6 for dates in 2003 and 2004, respectively.

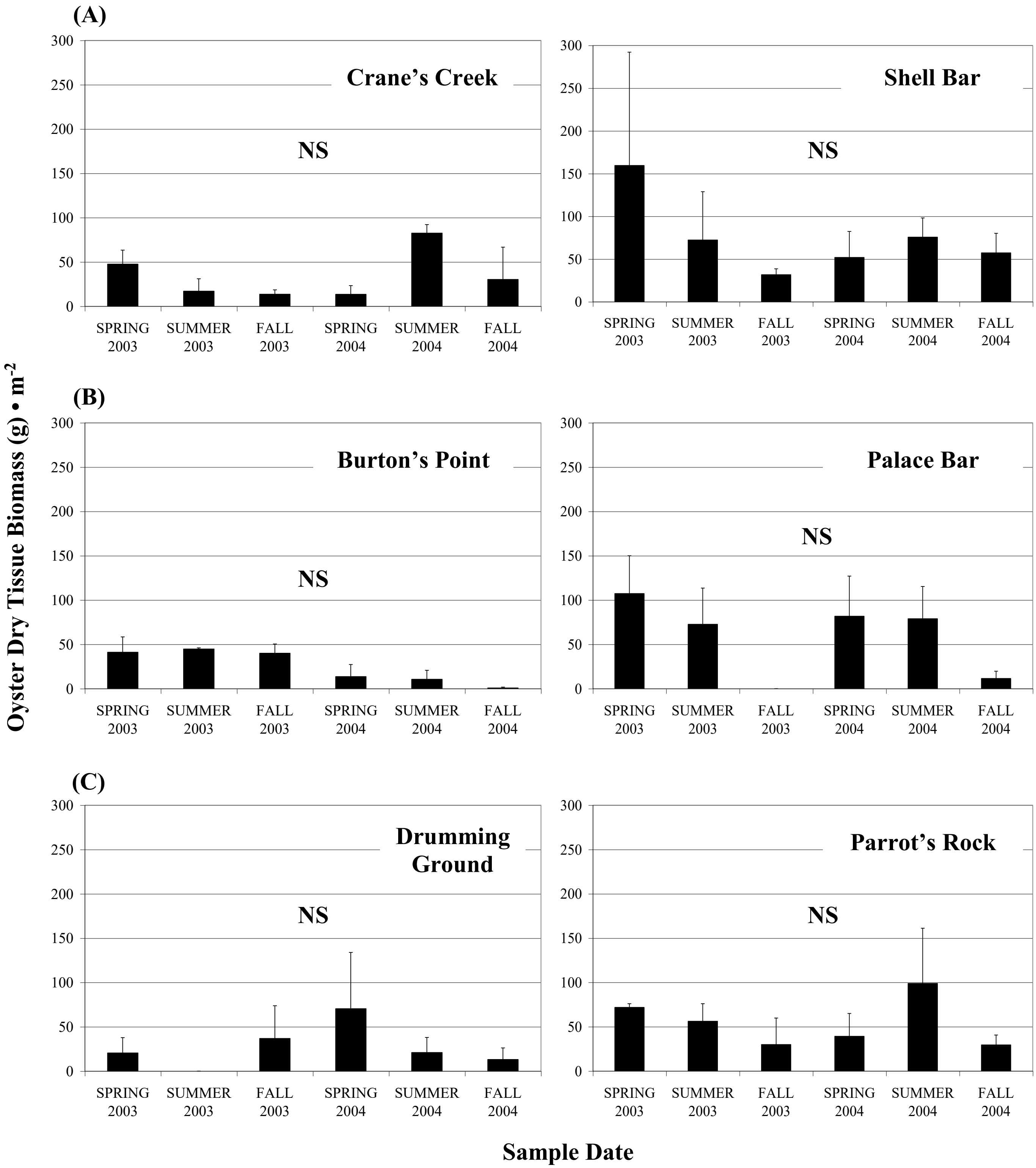


Figure 19. Size frequency distribution (shell height) for live oysters during the course of the study at Crane's Creek Reef for (A) 2003 and (B) 2004. The actual numbers of oysters • m^{-2} are reported on the x-axis and the scale is consistent for graphs for all reefs to allow for easy visual comparison. Values are aggregated in five mm intervals.

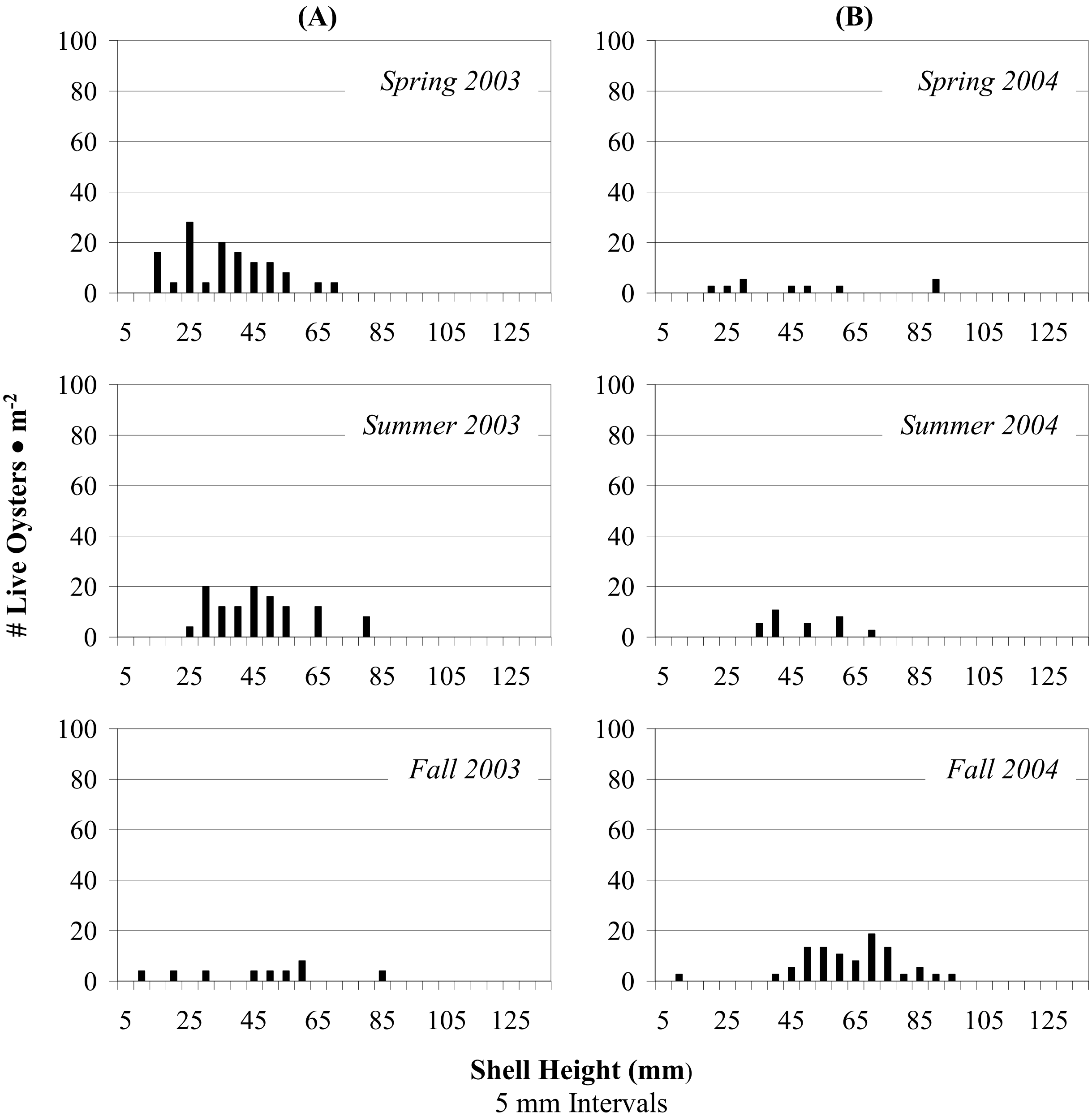


Figure 20. Size frequency distribution (shell height) for live oysters during the course of the study at Shell Bar Reef for (A) 2003 and (B) 2004. The actual numbers of oysters • m^{-2} are reported on the x-axis and the scale is consistent for graphs for all reefs to allow for easy visual comparison. Values are aggregated in five mm intervals.

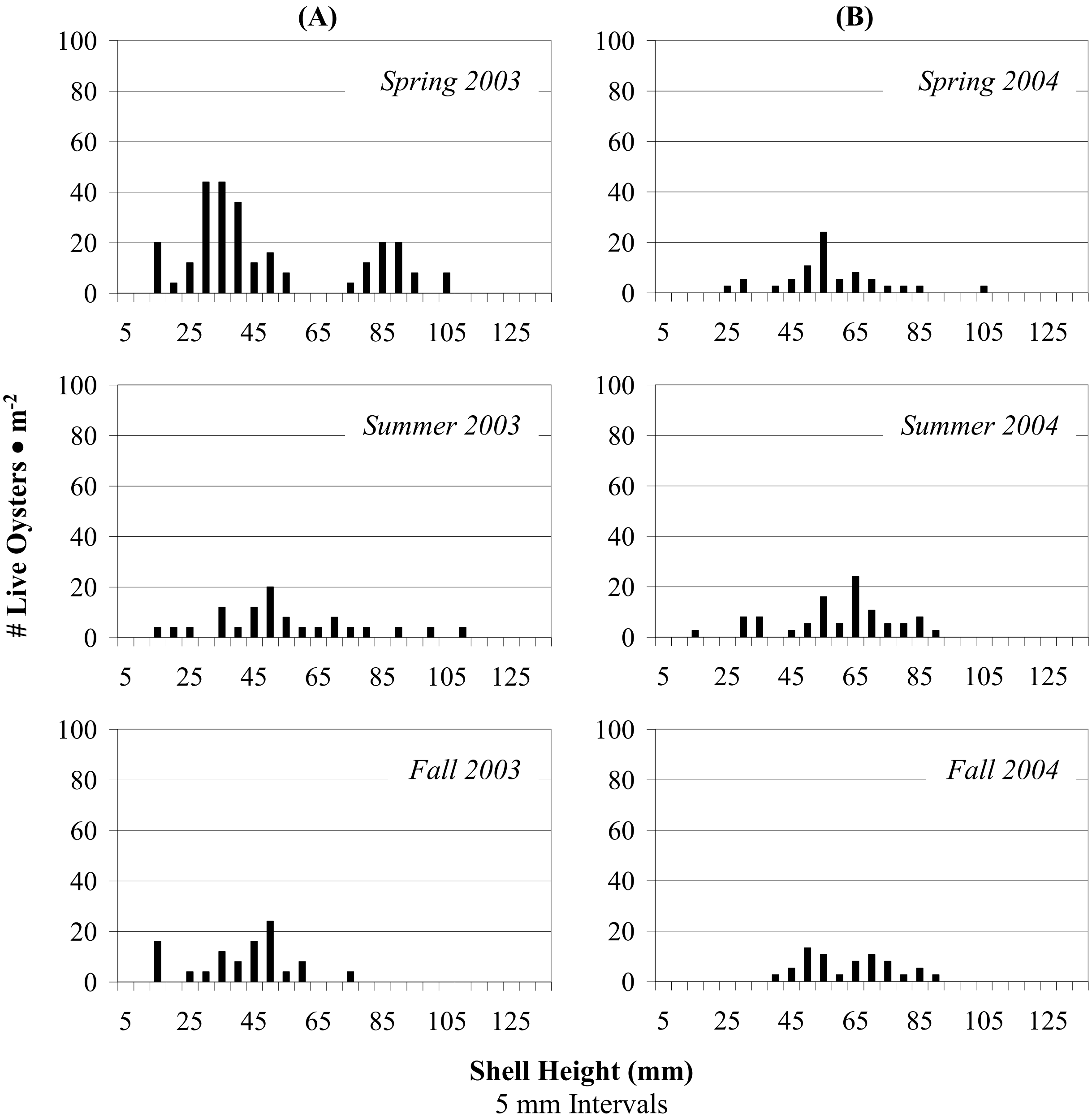


Figure 21. Size frequency distribution (shell height) for live oysters during the course of the study at Burton's Point Reef for (A) 2003 and (B) 2004. The actual numbers of oysters • m^{-2} are reported on the x-axis and the scale is consistent for graphs for all reefs to allow for easy visual comparison. Values are aggregated in five mm intervals.

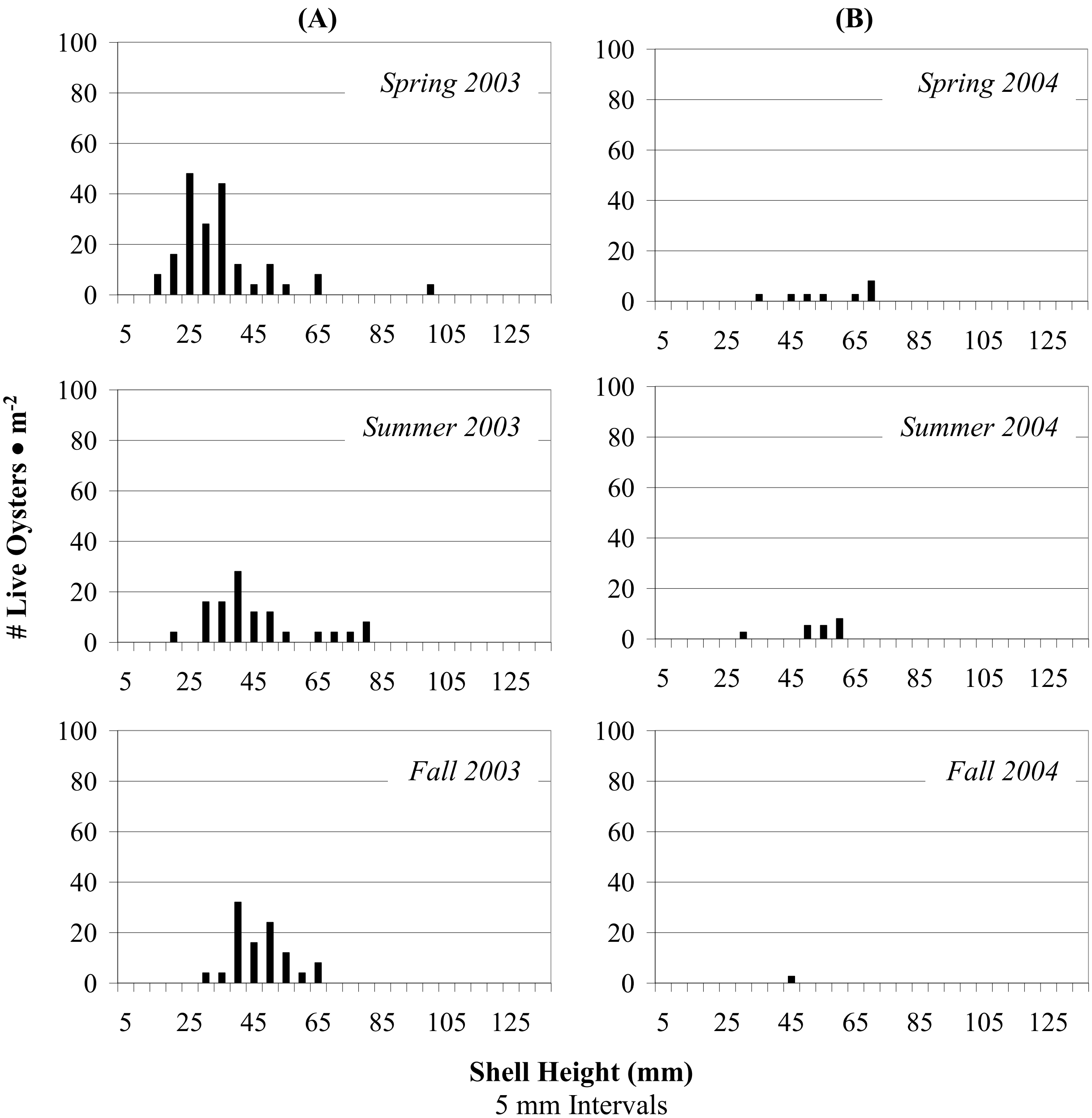


Figure 22. Size frequency distribution (shell height) for live oysters during the course of the study at Palace Bar Reef for (A) 2003 and (B) 2004. The actual numbers of oysters • m^{-2} are reported on the x-axis and the scale is consistent for graphs for all reefs to allow for easy visual comparison. Values are aggregated in five mm intervals.

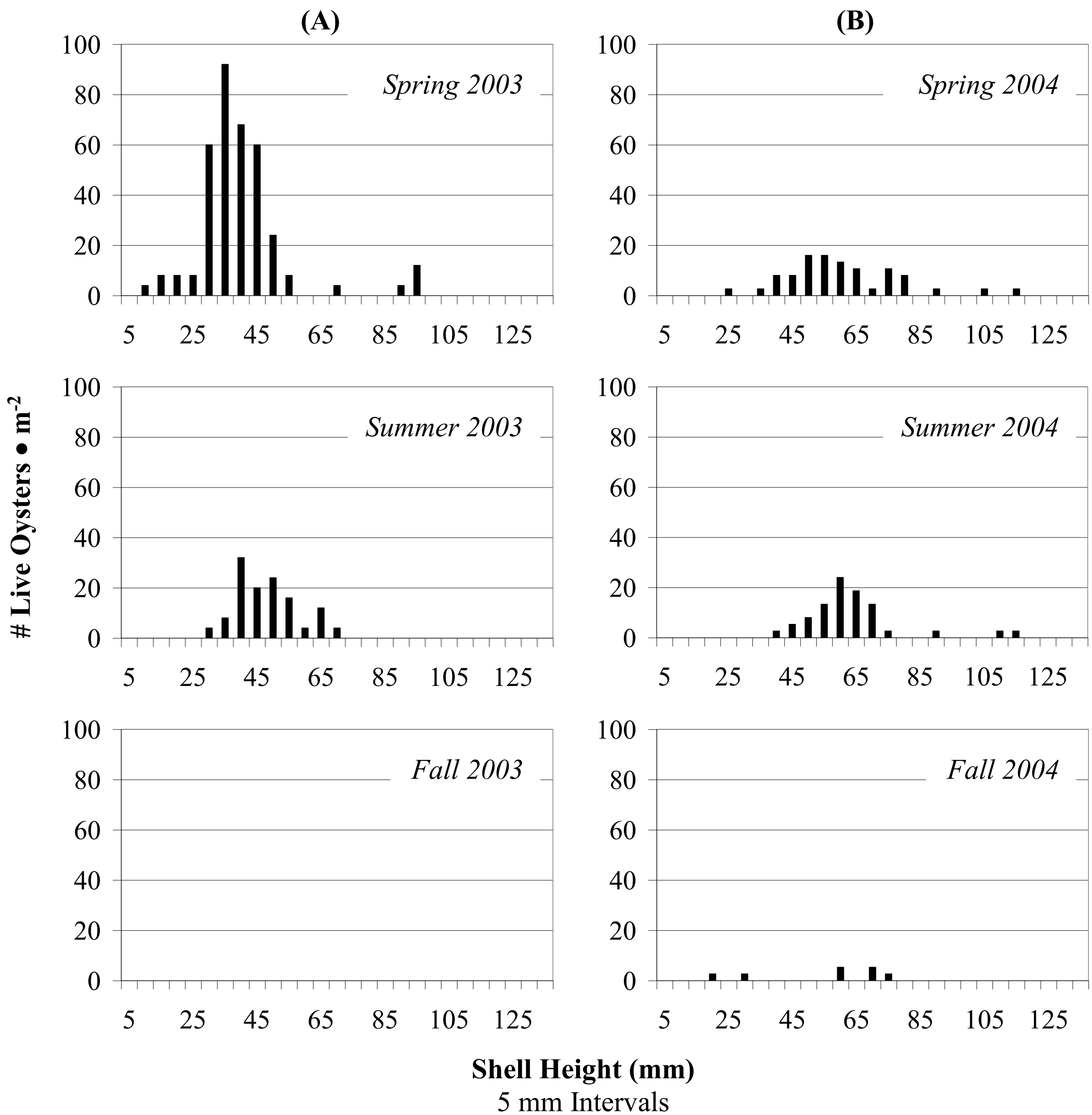


Figure 23. Size frequency distribution (shell height) for live oysters during the course of the study at Drumming Ground Reef for (A) 2003 and (B) 2004. The actual numbers of oysters • m^{-2} are reported on the x-axis and the scale is consistent for graphs for all reefs to allow for easy visual comparison. Values are aggregated in five mm intervals.

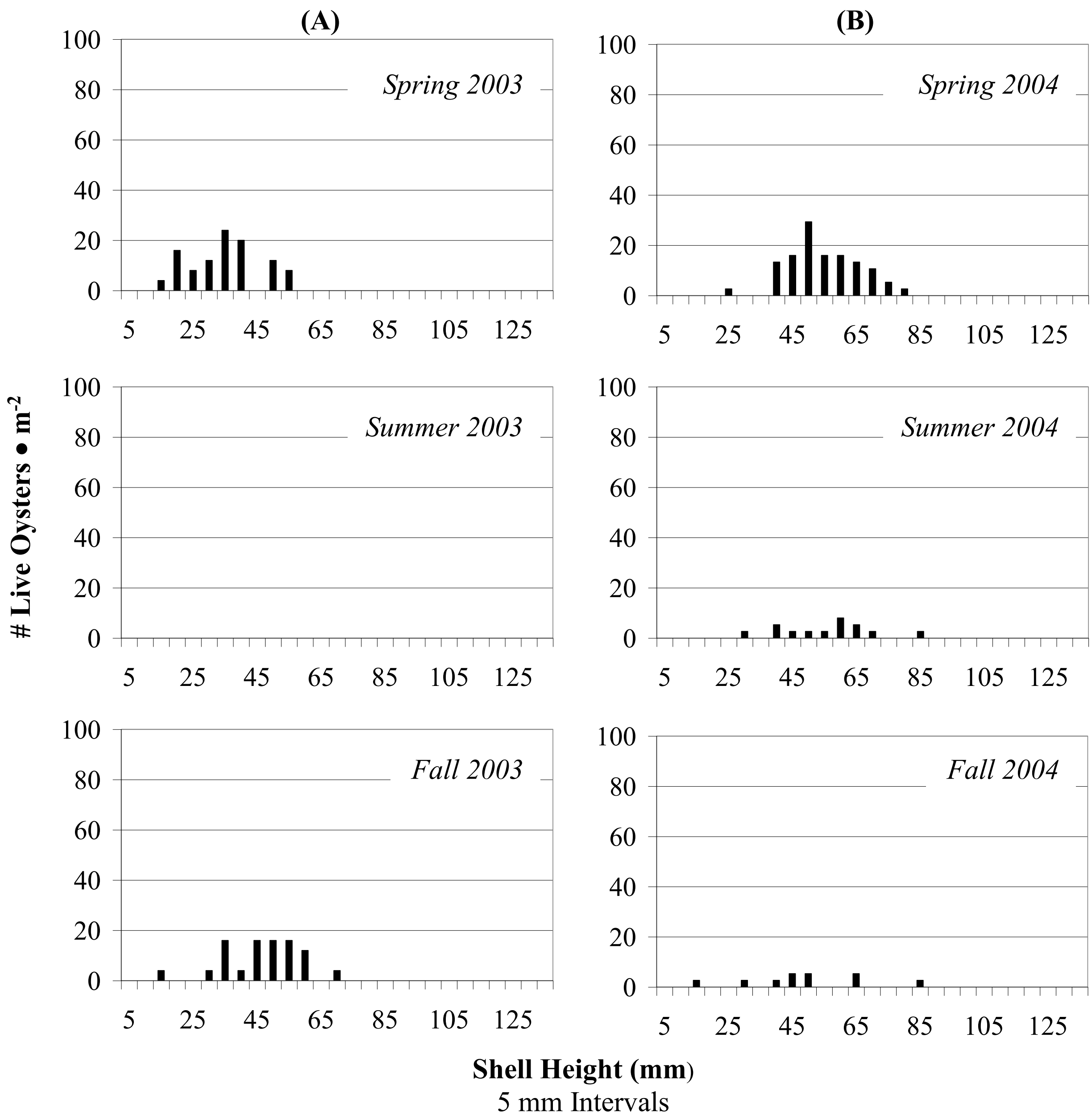
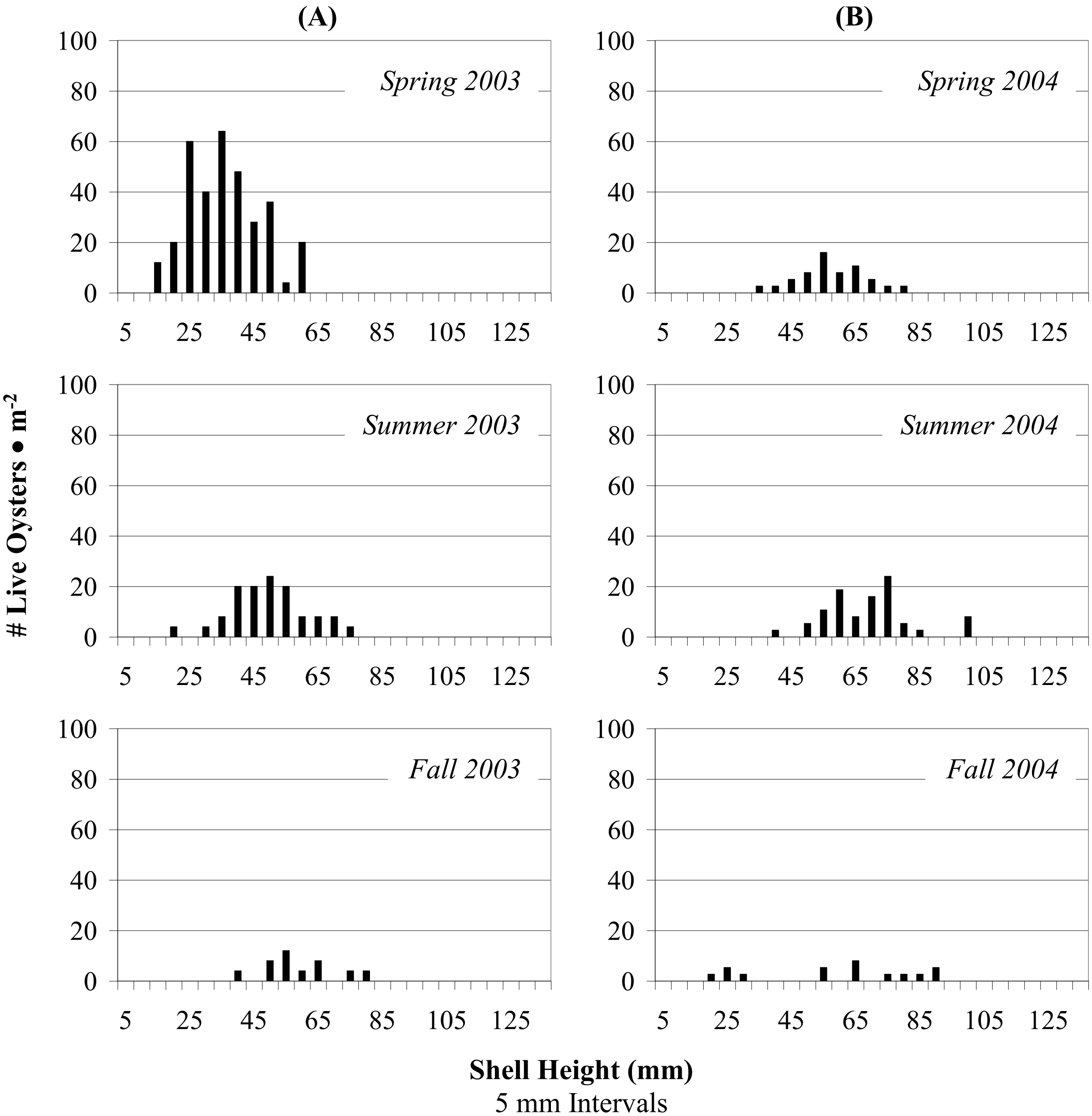


Figure 24. Size frequency distribution (shell height) for live oysters during the course of the study at Parrot's Rock Reef for (A) 2003 and (B) 2004. The actual numbers of oysters • m^{-2} are reported on the x-axis and the scale is consistent for graphs for all reefs to allow for easy visual comparison. Values are aggregated in five mm intervals.



Oyster size data met the assumptions of ANOVA so parametric statistical techniques were used for all analyses of these data. Significant main effects and interactions were observed for live and "box" oyster shell heights between *sample dates* and *reefs* when analyzed in a full factorial two-way ANOVA model (Appendix IX). Significant differences were observed for mean live oyster shell height between reefs when analyzed for individual seasons during spring 2003 ($p<0.0001$), fall 2003 ($p=0.0101$) and summer 2004 ($p=0.0003$). Although the temporal patterns in shell height were highly variable across most reefs over time, Parrot's Rock reef consistently ranked among the reefs with the largest oysters after the initial sampling in spring 2003 (Table 5). Shell height of "box" oysters exhibited significant differences between reefs for fall 2003 ($p=0.0334$), spring 2004($p=0.0127$) and fall 2004 ($p=0.0081$). Once again, although no dominant patterns were observed, Parrot's Rock tended to have larger "boxes" than some of the other reefs.

Significant differences were observed for mean live oyster shell height on individual reefs over time at Crane's Creek ($p<0.0001$), Shell Bar (0.0006), Burton's Point ($p<0.0001$), Palace Bar ($p<0.0001$), Drumming Ground (<0.0001) and Parrot's Rock ($p<0.0001$). A definite increasing trend was seen at both Crane's Creek and Shell Bar through the end of the study (Figure 25). However, shell height generally increased at all other reefs until the fall 2004 sample, when all exhibit a slight decrease in oyster size (Figure 25). "Box" shell height differed over time for Shell Bar ($p=0.0038$), Palace Bar ($p=0.0091$) and Parrot's Rock ($p=0.0481$), but did not at other reefs ($p>0.05$). However, no temporal trend was apparent, as means, ranging from 29.8-78.7, exhibited considerable variation (range: 1.9-16.8) typical of smaller sample sizes (range: 1-21). Significant main effects and interactions were observed for mean oyster ash-free dry tissue biomass between *sample dates* and *reefs* when analyzed in a

Table 5. Comparison of mean (SE) shell height (mm) of live oysters between reefs[a] for each sample date for (A) 2003 and (B) 2004. Reefs are listed in descending order of oyster abundance for each date and "n" in the table refers to the number of oysters measured from each sample to determine means. Where significant differences were observed (p<0.05), means with different letters were significantly different within each individual sample date (quadrate n=4 for each reef for 2003 and n=6 for each reef for 2004).

(A)

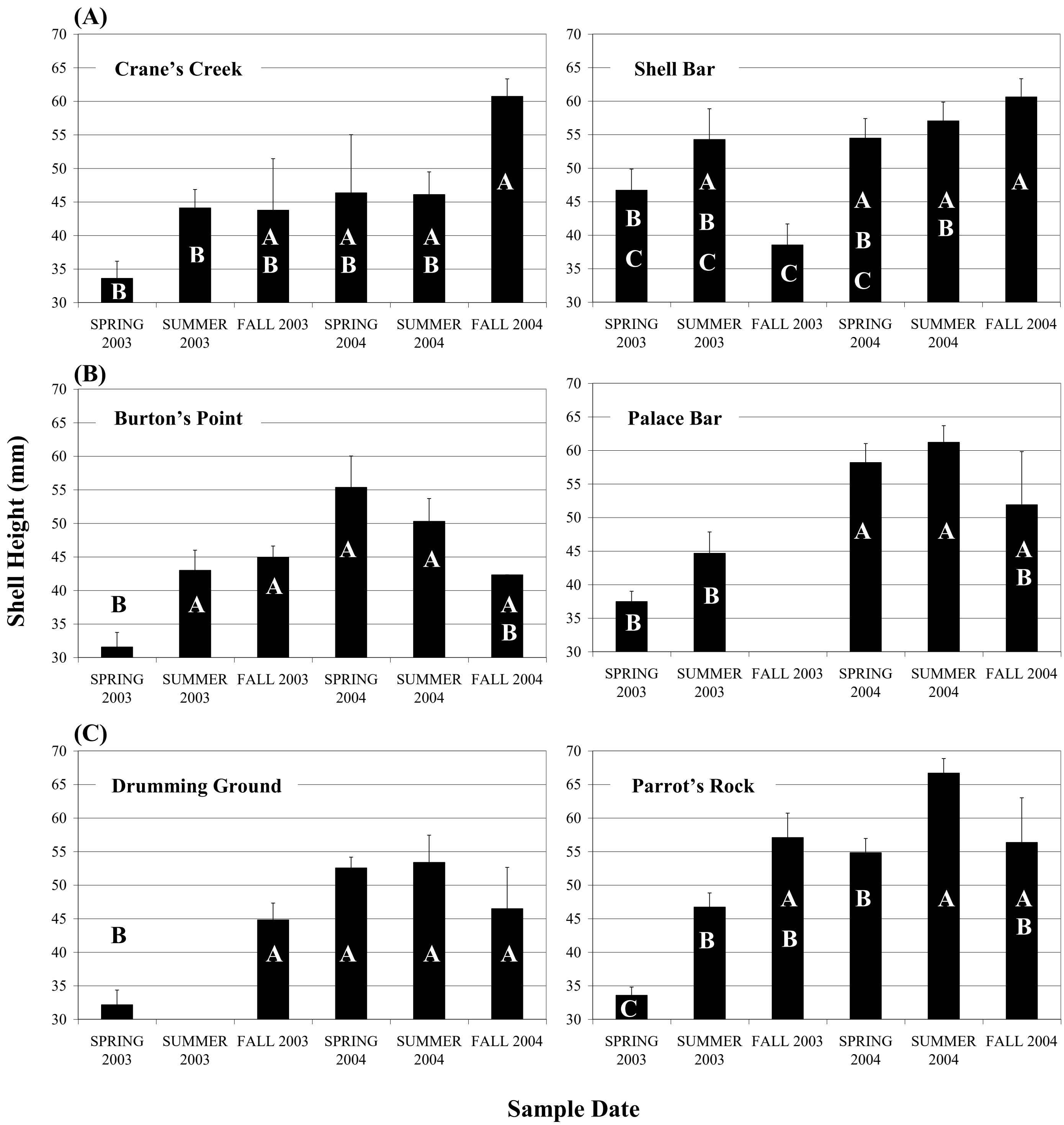
Spring 2003**			Summer 2003^{NS}			Fall 2003*		
Reef	**n**	**Mean (SE)**	**Reef**	**n**	**Mean (SE)**	**Reef**	**n**	**Mean (SE)**
SB	67	46.7 (3.2)^{A}	SB	40	54.2 (4.6)	PR	11	57.1 (3.6)^{A}
PB	90	37.5 (1.5)^{B}	PR	36	46.7 (2.1)	BP	26	44.9 (1.7)^{A,B}
CC	32	33.6 (2.6)^{B}	PB	45	44.7 (3.2)	DG	23	44.8 (2.5)^{A,B}
PR	83	33.6 (1.2)^{B}	CC	39	44.1 (2.8)	CC	9	43.7 (7.7)^{A,B}
DG	26	32.1 (2.2)^{B}	BP	31	43.0 (3.0)	SB	25	38.5 (3.1)^{B}
BP	47	31.5 (2.2)^{B}	DG	0	-	PB	0	-

(B)

Spring 2004^{NS}			Summer 2004**			Fall 2004^{NS}		
Reef	**n**	**Mean (SE)**	**Reef**	**n**	**Mean (SE)**	**Reef**	**n**	**Mean (SE)**
PB	40	58.2 (2.8)	PR	38	66.7 (2.2)^{A}	CC	38	60.7 (2.6)
BP	8	55.3 (4.7)	PB	38	61.2 (2.5)^{A}	SB	27	60.6 (2.7)
PR	24	54.8 (2.1)	SB	39	57.0 (2.8)^{A,B}	PR	14	56.3 (6.7)
SB	30	54.4 (2.9)	DG	13	53.4 (4.1)^{A,B}	PB	7	51.9 (7.9)
DG	47	52.5 (1.6)	BP	9	50.3 (3.4)^{A,B}	DG	10	46.5 (6.2)
CC	9	46.3 (8.7)	CC	12	46.1 (3.4)^{B}	BP	1	42.3 (-)

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock
^{NS} indicates 'No Significant Difference' between reefs
* indicates means were significantly different, p<0.05, between reefs for this sample date
** indicates means were significantly different, p<0.01, between reefs for this sample date

Figure 25. Mean (+SE) live oyster shell height (mm) over time for individual reefs in (A) Great Wicomico River, (B) Piankatank River and (C) Rappahannock River. Within each reef's graph, NS indicates no significant differences between dates, while means with different letters are significantly different (P<0.05). For each individual reef n=4 and n=6 for dates in 2003 and 2004, respectively (i.e. number of quadrate samples; see Table 5 for actual number of oyster measurements comprising means).



factorial two-way ANOVA model (Appendix IX). Significant differences were observed for mean live oyster ash-free dry tissue biomass between reefs when analyzed by season (Table 6) during spring 2003 ($p<0.0001$), fall 2003 ($p=0.0065$) and summer 2004 ($p=0.0022$).

Significant differences were observed for mean biomass of individual oysters over time at all individual reefs: Crane's Creek ($p<0.0001$), Shell Bar (0.0349), Burton's Point ($p=0.0035$), Palace Bar ($p<0.0001$), Drumming Ground (<0.0001) and Parrot's Rock ($p<0.0001$). An increasing trend was seen at Crane's Creek, Palace Bar, Drumming Ground and Parrot's Rock through the end of the study (Figure 26). However, these differences are less striking than those for oyster shell height.

Oyster Settlement

Oyster settlement data were normalized for tile surface area and varying deployment durations and are reported as the number of oysters • m^{-2} • $week^{-1}$. Oyster settlement was very low in 2003 at all reefs except those in the Great Wicomico River (Figure 27). Settlement was first recorded during the two weeks prior to August 8th (Palace Bar, Piankatank River), generally peaked during late-August/early-September and diminished to near zero by late-September (Appendices X-XII). Timing was comparable at all sites (Figure 27); however, mean weekly settlement was significantly higher at Shell Bar and Crane's Creek reefs ($p<0.0001$; Appendix XIII) than at other reefs, which were similar (Table 7).

Compared to 2003, oyster settlement in 2004 was relatively lower in the Great Wicomico River, higher in the Piankatank River and similar in the Rappahannock River (Figure 27). Two settlement peaks were observed at the Great Wicomico and Piankatank reefs, but only one peak was evident at the Rappahannock reefs (Figure 27). Settlement was first recorded during the two weeks prior to July 21st (Shell Bar, Great Wicomico River),

Table 6. Comparison of mean (SE) ash-free dry tissue biomass (mg) of individual live oysters between reefs[a] for each sample date for (A) 2003 and (B) 2004. Reefs are listed in descending order for each date and "n" in the table refers to the number of oysters measured from each sample to determine means. Where significant differences were observed (p<0.05), means with different letters were significantly different within each individual sample date (quadrate n=4 for each reef for 2003 and n=6 for each reef for 2004).

(A)

Spring 2003**			**Summer 2003^{NS}**			**Fall 2003****		
Reef	**n**	**Mean (SE)**	**Reef**	**n**	**Mean (SE)**	**Reef**	**n**	**Mean (SE)**
SB	26	595.4 (85.5)^{A}	SB	25	723.6 (144.9)	PR	11	679.6 (100.6)^{A}
PB	83	298.0 (3.7)^{B}	PB	38	478.2 (127.9)	CC	9	473.8 (155.2)^{A,B}
CC	47	237.1 (37.9)^{B}	PR	32	439.2 (44.5)	DG	23	400.9 (45.3)^{B}
BP	32	218.5 (48.6)^{B}	CC	29	410.0 (61.6)	BP	26	385.2 (34.2)^{B}
PR	90	216.4 (17.4)^{B}	BP	28	399.4 (70.3)	SB	25	317.6 (50.9)^{B}
DG	67	197.2 (28.9)^{B}	DG	0	-	PB	0	-

(B)

Spring 2004^{NS}			Summer 2004**			**Fall 2004^{NS}**		
Reef	**n**	**Mean (SE)**	**Reef**	**n**	**Mean (SE)**	Reef	**n**	**Mean (SE)**
PB	40	766.7 (94.0)	PR	38	975.5 (75.6)^{A}	CC	38	814.9 (71.6)
SB	30	648.7 (87.6)	PB	36	822.4 (95.7)^{A,B}	SB	27	796.0 (82.0)
BP	8	640.3 (110.6)	SB	39	727.8 (70.5)^{A,B}	PR	14	791.3 (161.7)
PR	24	612.5 (53.2)	DG	13	605.2 (101.2)^{A,B}	PB	7	618.3 (149.2)
CC	9	568.2 (217.9)	BP	8	498.0 (61.9)^{A,B}	DG	10	492.6 (138.3)
DG	47	561.9 (39.7)	CC	12	423.5 (72.5)^{B}	BP	1	317.2 (-)

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock
^{NS} indicates 'No Significant Difference' between reefs
* indicates means were significantly different, p<0.05, between reefs for this sample date
** indicates means were significantly different, p<0.01, between reefs for this sample date

Figure 26. Mean (+SE) individual live oyster ash-free dry tissue biomass (mg) over time for individual reefs in (A) Great Wicomico River, (B) Piankatank River and (C) Rappahannock River. Within each reef's graph, NS indicates no significant differences between dates, while means with different letters are significantly different (P<0.05; see Table 6 for actual number of oyster measurements comprising means).

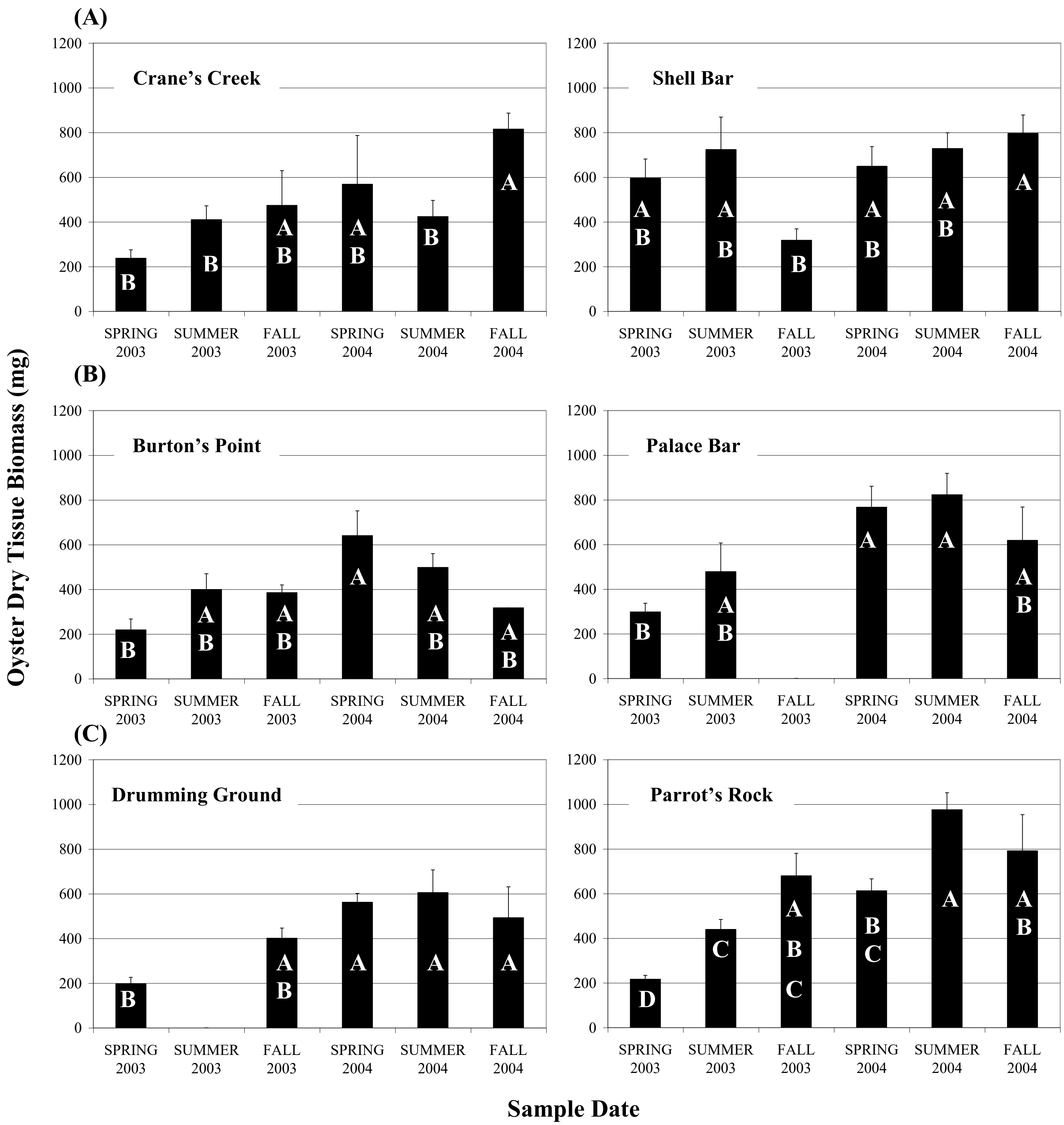
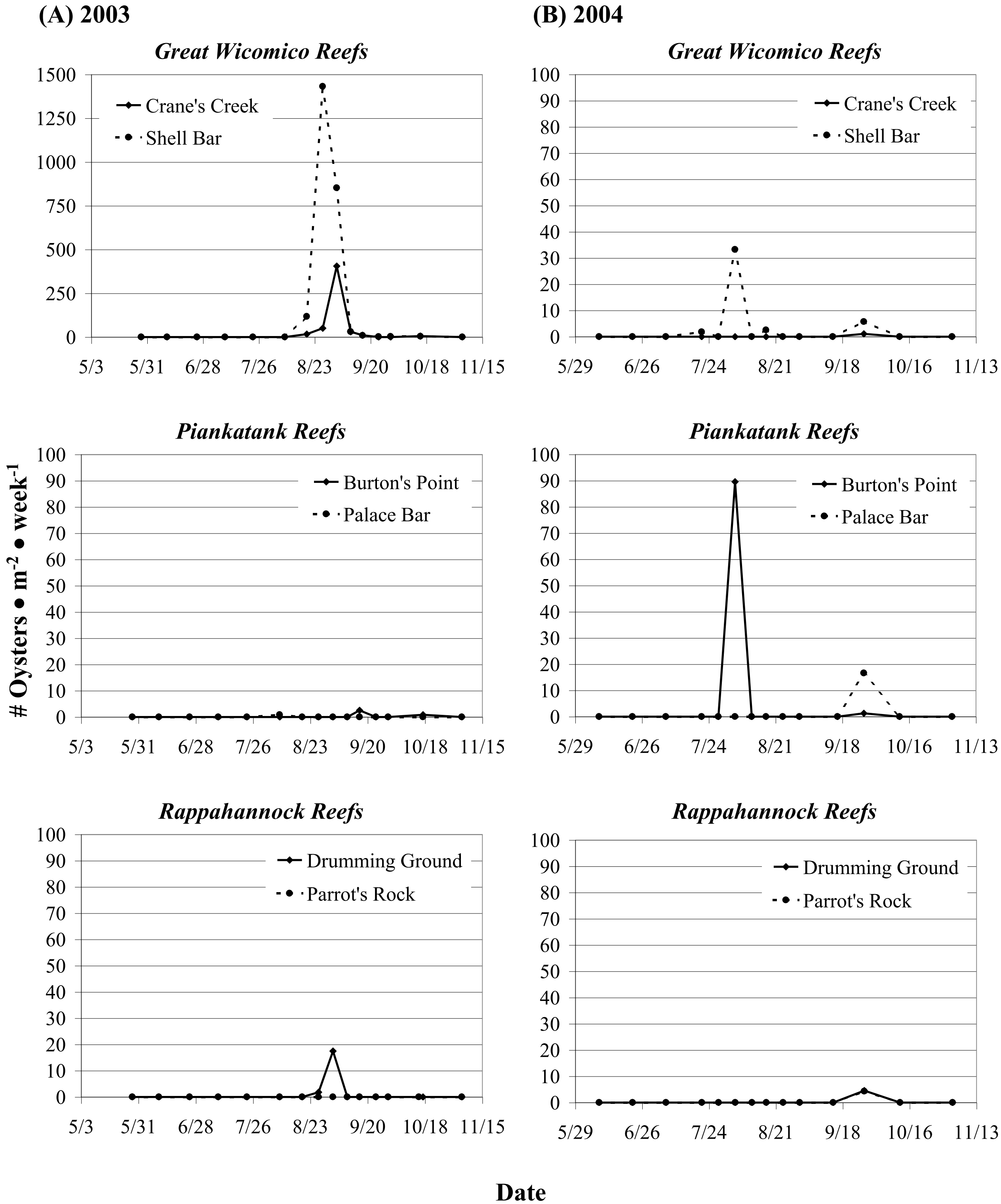


Figure 27. Area and time standardized mean oyster settlement (oysters • m^{-2} • week^{-1}) for reefs during (A) 2003 and (B) 2004. Note that axis scales are similar for all but 2003 Great Wicomico reefs do to the extreme difference in settlement (see Appendix IX-XI for details on means and SE).



generally peaked in early August and mid-September and diminished to near zero by early-October (Appendices X-XII). Timing was comparable at all sites (Figure 27); however, mean weekly settlement was significantly different between reefs ($p=0.0374$; Appendix XIII; Table 7). Although a significant difference was measured in the overall model, an *a posteriori* multiple comparison (Tukey's) could not differentiate between means.

Although mean settlement per unit time was used to compare reefs, cumulative settlement was estimated for each reef for 2003 and 2004 (Table 7). These numbers represent an index of the total area standardized number of oysters expected to have settled on reefs during an entire settlement season and ranged from 2,450 • m^{-2} at Shell Bar reef in 2003 to 0 • m^{-2} at Parrot's Rock reef in 2003.

Oyster Disease

All six reefs showed the presence of *P. marinus*, while one showed the presence of *H. nelsoni* for 2004 samples (Table 8). Prevalence of *P. marinus* ranged from 48-76% and the intensity of infection was generally moderate to light. Reefs in the Great Wicomico River (Crane's Creek and Shell Bar reefs) appeared to have slightly lower disease prevalence than other tributaries in 2004.

Prevalence of *P. marinus* was lower on the reefs in 2004 compared with data available for four of the same reefs from 2003 (collected as part of other monitoring programs; Table 8). Prevalence of *H. nelsoni* was likely low to non-existent in both years due to low salinity from above average rainfall (Figure 2).

Table 7. Area and time standardized mean (SE) oyster settlement (oysters • m^{-2} • $week^{-1}$) and cumulative settlement (total oysters • m^{-2}) for reefs during 2003 and 2004. Means with different letters were significantly different within each year (n=60 for each reef for 2003 and n=52 for each reef for 2004). Note that even though a significant difference between reefs for 2004 was observed, an *a posteriori* multiple comparison (Tukey's) could not differentiate between reefs.

Year	Reef[a]	Mean (SE)			Cumulative
2003**	SB	163.33	(53.56)	A	2450
	CC	34.59	(14.77)	A	519
	DG	1.29	(0.58)	B	19
	BP	0.23	(0.18)	B	3
	PB	0.06	(0.06)	B	1
	PR	0.00	(0)	B	0
2004*	BP	6.99	(4.2)	A	91
	SB	3.33	(1.68)	A	43
	PB	1.28	(1.28)	A	17
	DG	0.35	(0.28)	A	5
	PR	0.33	(0.16)	A	4
	CC	0.08	(0.08)	A	1

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock
* indicates means were significantly different, $p<0.05$, between reefs for 2004
** indicates means were significantly different, $p<0.01$, between reefs for 2003

Table 8. Disease causing organism prevalence and intensity in oysters sampled from each reef site during (A) 2003 (four of six reefs as part of several other projects for comparison to 2004) and (B) 2004 (as part of this study). H=heavy, M=moderate, L=light.

(A)

Site	*H. nelsoni*		*P. marinus*	
	Prevalence %	**Intensity H-M-L**	**Prevalence %**	**Intensity H-M-L**
Crane's Creek	-	-	-	-
Shell Bar	-	-	-	-
Burton's Point	0	0-0-0	88	5-10-7
Palace Bar	0	0-0-0	92	0-7-16
Drumming Ground	0	0-0-0	88	1-13-8
Parrot's Rock	0	0-0-0	88	2-10-10

(B)

Site	*H. nelsoni*		*P. marinus*	
	Prevalence %	**Intensity H-M-L**	**Prevalence %**	**Intensity H-M-L**
Crane's Creek	0	0-0-0	48	1-3-8
Shell Bar	0	0-0-0	60	1-7-7
Burton's Point	0	0-0-0	68	1-4-12
Palace Bar	0	0-0-0	68	0-10-7
Drumming Ground	1	0-0-1	64	2-7-7
Parrot's Rock	0	0-0-0	76	5-9-5

Epifaunal Community

Eighteen taxa of sessile organisms were collected and enumerated in quadrate samples (Table 9). Numerically dominant species (exclusive of oysters, which were discussed above) were ribbed mussels (G*eukensia demissa*), white crust (*Membranipora tenuis*) and barnacles (*Balanus* spp.). Not all taxa were found at all reefs and species/taxa richness ranged from 12 at Crane's Creek and Palace Bar reefs to 6 at Drumming Ground reef (Table 9).

Appendices XIV and XV contain data on the abundances of total epifauna and selected species by reef and sample date. For some taxa, individuals were counted, whereas it was more appropriate to estimate aerial coverage for others (see Table 2). We analyzed the total abundance of non-oyster groups that were counted (reported as $\# \bullet m^{-2}$) and the total aerial coverage of non-oyster groups (reported as % cover), exclusive of white crust (*M. tenuis*). White crust is an encrusting colonial bryozoan that dominated this category. Therefore, we separated this taxonomic group from the others to provide better resolution of the results pertaining to possible food or space competition with oysters. We further analyzed for differences in ribbed mussel abundance and barnacle cover by reef and sample date. Other groups were not analyzed separately due to their rarity in samples (Table 9).

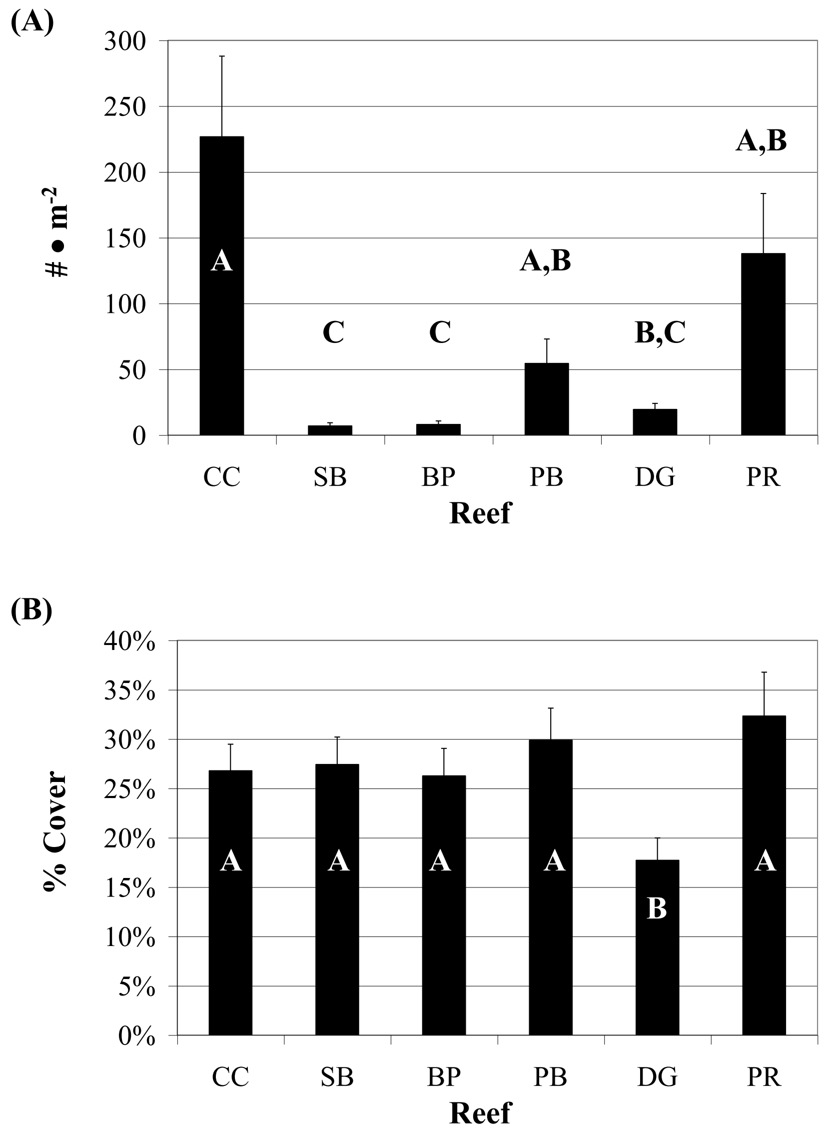
Total abundance of non-oyster taxa (# and % cover) and specific abundance measures for ribbed mussels, barnacle and white crust all exhibited significant differences for *sample dates* and *reefs* (Appendix XVI). However, because we were not necessarily interested in specific hypotheses regarding seasonality of these species, but rather their potential direct or indirect impacts on the oyster population, we pooled data for all dates to compare reefs rather than analyze each date separately. The overall abundance (#) of epifauna was highest at Crane's Creek and Parrot's Rock and lowest at Shell Bar and Burton's Point (Figure 28).

Table 9. Total abundance or overall mean % cover of non-oyster taxa collected in quadrate samples during the course of the project at all study reefs[a]. Absence of taxa are indicated by blank cells. Overall richness for each reef is also noted.

Species	Total #	CC	SB	BP	PB	DG	PR
Ribbed Mussel *Geukensia demissa*	783	412	11	9	77	29	245
Dwarf Surf Clam *Mulinia lateralis*	20	13			7		
Flat worm *Stylocus* spp.	15		1	3	1		10
Slipper Shell *Crepidula fornicata*	5				5		
Anemone likely *Haliplanella luciae*	4			2	2		
Baltic Macoma *Macoma balthica*	1				1		
Hard Clam *Mercenaria mercenaria*	1		1				
	% Coverage						
White Crust *Membarnipora tenuis*	16.1	23.5	23.0	14.2	12.3	13.3	10.4
Barnacle *Balanus* spp.	7.6	5.1	7.6	7.2	9.4	3.9	12.4
Red Beard Sponge *Microciona prolifera*	0.5	0.4	0.1	1.1	<0.1	0.3	1.1
Fan Worm *Hydroides dianthus*	0.4	0.5	0.6	0.3	0.3	0.1	0.3
Sea Grape *Molgula manhattensis*	0.1			0.1		0.3	0.1
Boring Sponge *Cliona* spp.	<0.1	0.1		0.2			
Hydroid likely *Ectopleura* spp.	<0.1	<0.1					
Red Algae *Ceramium* spp.	0.6	0.9	0.4		1.1		<0.1
Green Algae *Enteromorpha* spp.	0.1	0.3	0.1		<0.1		
Green Algae *Cladophora* spp.	<0.1	<0.1	<0.1				
Red Algae *Polysiphonia* spp.	<0.1	<0.1	<0.1				
	Richness	12	11	9	12	6	8

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Figure 28. Mean (+SE) abundance of selected metrics for non-oyster epibenthic organisms: (A) total non-oyster abundance (# • m^{-2}) and (B) non-*Membranipora tenuis* abundance (% cover). Means with different letters are significantly different (P<0.05). Data are pooled for all sample dates in 2003 and 2004 for each reef. See Table 2 for taxa included in the respective abundance measurements. Reef abbreviations follow those in Table 1.



Ribbed mussels essentially drove this pattern, as they were the dominant species, often accounting for >90% of the epifauna. Overall aerial coverage (% cover) of epifauna, exclusive of white crust, was always <33% and was significantly lower at Drumming Ground (p<0.0001) than the other reefs which were equal (Figure 28).

White crust % cover was significantly higher at Shell Bar (x=46, SE=4) and Crane's Creek (x=46, SE=5) reefs than at Parrot's Rock (x=28, SE=4), but all other reefs were equal to both groups. Barnacle % cover was significantly higher at Parrot's Rock (x=29, SE=4) and Palace Bar (x=26, SE=3) reefs than at Drumming Ground (x=16, SE=2), with all other reefs not differing from either group.

Significant differences were observed over time for non-oyster epifauna for all reefs but Drumming Ground (Table 10). Although quite variable, general downward trends were observed for Crane's Creek, Shell Bar, Burton's Point and Parrot's Rock reefs (Figure 29).

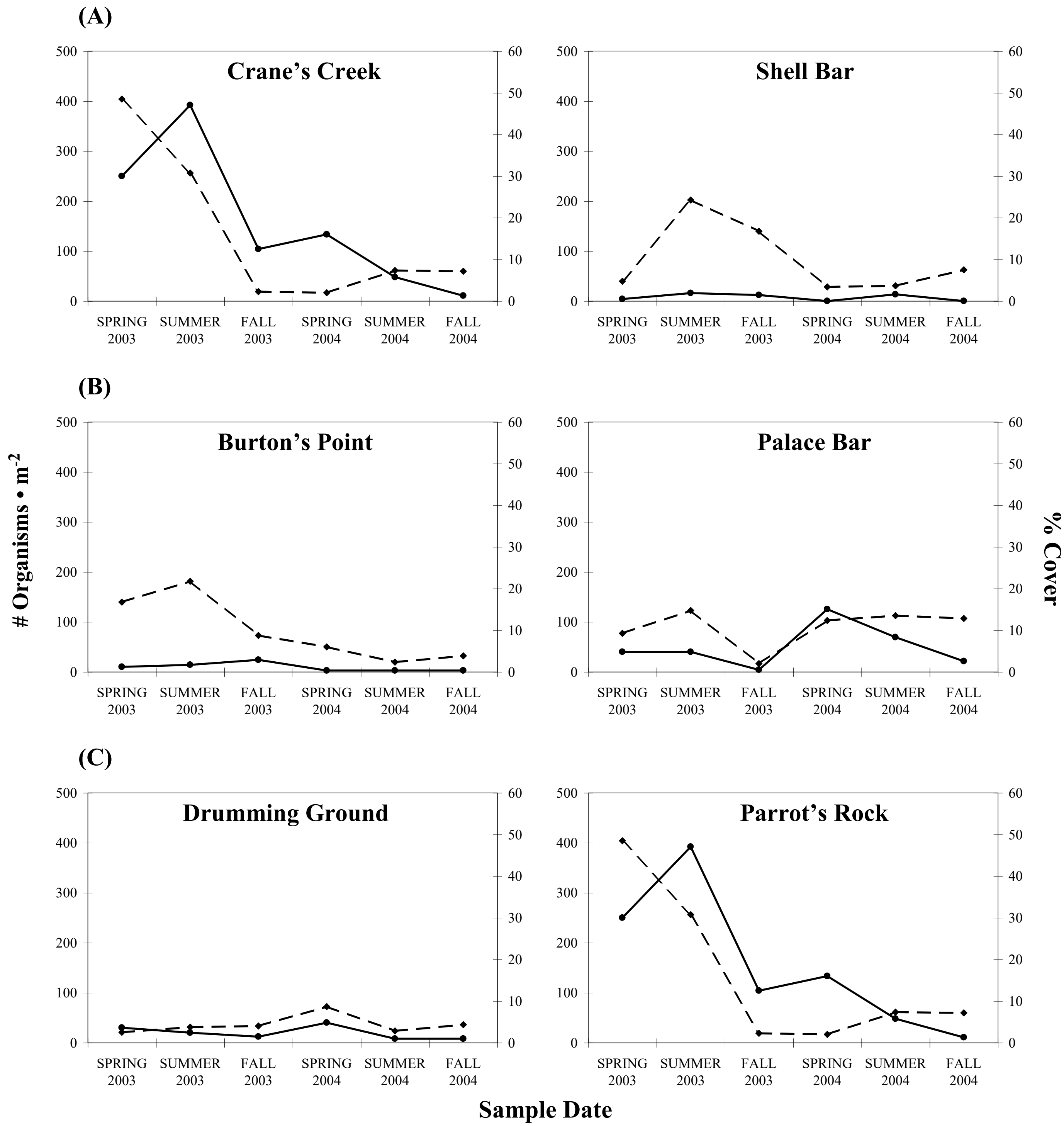
Table 10. Comparison of study reefs over time with respect to total non-oyster abundance for taxa quantified by # • m^{-2} and % cover. P-values refer to differences between sample dates for each individual reef (see Table 2 for taxa included in each category).

	P-Value	
Reef	**# • m^{-2}**	**% Cover**
Crane's Creek	0.0746	***<0.0001***
Shell Bar	0.1363	***0.0001***
Burton's Point	0.1851	***0.0012***
Palace Bar	0.1133	***0.0440***
Drumming Ground	0.0974	0.6855
Parrot's Rock	***0.0059***	***<0.0001***

<u>Physical Attributes of Reefs</u>

Depth and Slope – Although all reefs in this study were designed and constructed in a similar manner, some differences were observed in their gross and fine architectural characteristics. Significant differences were observed for seabed depth around reefs (p=0.0009) and reef crest depths (p=0.0004). Drumming Ground and Burton's Point reefs were in slightly deeper water, than the other reefs (Table 11). The average slope of reefs

Figure 29. Mean density (exclusive of oysters) (solid bar; # • m^{-2}) and percent cover (exclusive of *Membranipora tenuis*) (dashed line; % cover) for epifaunal taxa (see Table 2 for taxa included in each group) over time for individual reefs in (A) Great Wicomico River, (B) Piankatank River and (C) Rappahannock River. For each individual reef, n=4 and n=6 for dates in 2003 and 2004, respectively.



ranged from 18.7 % at Parrot's Rock to 9.8 % at both Burton's Point and Palace Bar, however no significant differences were detected (p=0.1237; Table 11).

Table 11. Mean (SE) seabed depth (m), reef crest depth (m) and reef slope (%) of reefs[a]. Reef means with different letters were significantly different. Sample sizes at each reef for seabed, reef crest and slope were 10, 6 and 12, respectively.

Seabed Depth**			Reef Crest Depth**			Reef Slope[NS]		
DG	3.26	(0.12)[A]	BP	1.79	(0.15)[A]	PR	18.7	(3.6)
BP	3.09	(0.10)[A,B]	DG	1.54	(0.07)[A,B]	SB	14.8	(2.7)
PR	3.06	(0.06)[A,B,C]	PR	1.45	(0.05)[A,B,C]	CC	11.0	(1.1)
PB	2.39	(0.14)[B,C]	CC	1.22	(0.10)[B,C]	DG	10.3	(1.4)
SB	2.38	(0.30)[B,C]	SB	0.99	(0.20)[B,C]	BP	9.8	(1.2)
CC	2.34	(0.27)[C]	PB	0.85	(0.15)[C]	PB	9.8	(1.3)

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock
[NS] indicates means were not significantly different, p>0.05, between reefs
** indicates means were significantly different, p<0.01, between reefs

Particle Characteristics – Particle characteristic means are summarized for % oyster shell (i.e. not clam or other shell) and % boring sponge damage for samples at each reef during each sample period in Appendix XVII. Overall, oyster shell composed >95% of reef surface particles at all reefs except Drumming Ground and Parrot's Rock (Table 12). The reefs with lower proportion of oyster shells (~77 %) showed higher variation than other reefs, a result of some samples being taken from individual reef mounds composed almost entirely of surf clam shell. Samples from other mounds at those reefs were predominately oyster shell. No statistically significant differences were observed in mean % of oyster shells across

Table 12. Prevalence (%) of reef particles that were oyster shell and particles that exhibited evidence of boring sponge (*Cliona* spp.) damage. Reef means with different letters were significantly different. Means (SE) are pooled for all sample dates for each reef. For each reef n=30.

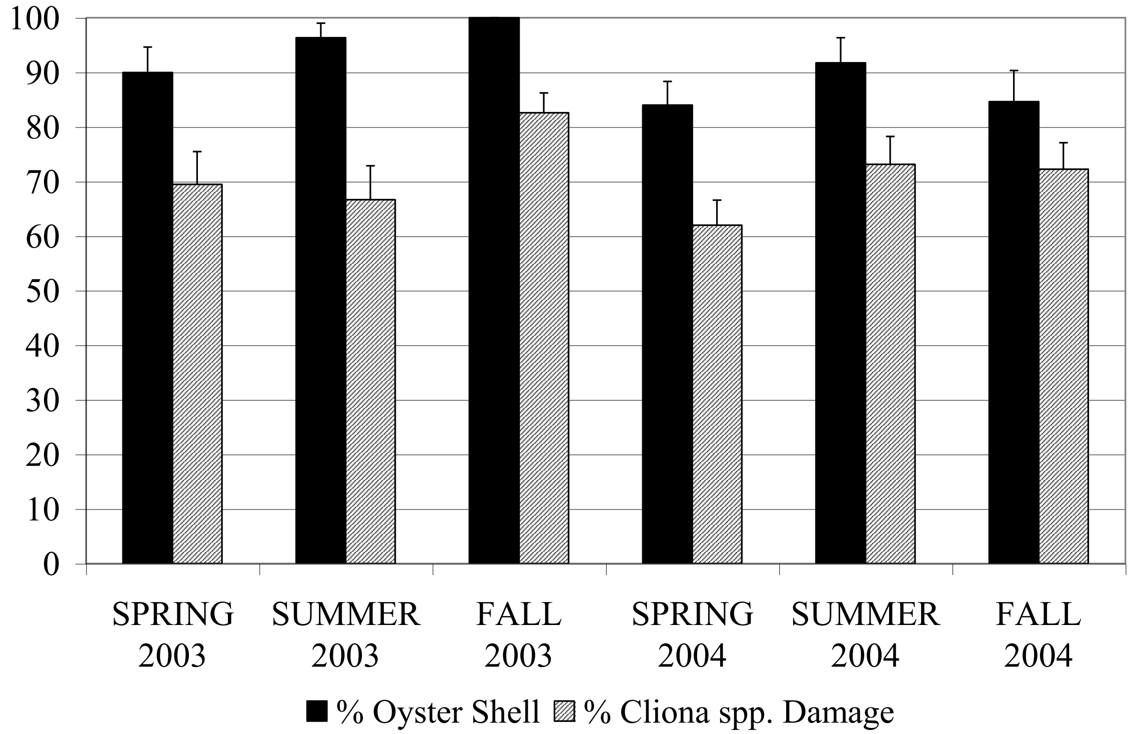
% Oyster Shell[NS]			% *Cliona* spp.**		
BP	97.5	(0.7)	CC	86.9	(2.9)[A]
CC	97.2	(1.4)	BP	78.7	(2.8)[A]
PR	96.8	(1.0)	SB	78.2	(3.6)[A]
SB	96.1	(2.3)	PR	74.4	(3.5)[A]
DG	77.3	(7.1)	PB	72.6	(5.2)[A]
PB	76.6	(7.3)	DG	33.1	(5.9)[B]

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock
[NS] indicates means were not significantly different, p>0.05, between reefs
** indicates means were significantly different, p<0.01, between reefs

reefs (p=0.0698; Appendix XIII). Significant differences were observed in this measure over time (Figure 30). These differences appear to be an artifact of fall 2003 samples containing 100% oyster shell leading to no variation. Because of this, we did not further analyze % oyster shell over time for each individual reef.

The prevalence of reef particles exhibiting boring sponge damage was significantly different between reefs (p<0.0001) with Drumming Ground having much less damage than the other reefs, which were equal (Table 12). Overall, *Cliona* prevalence varied over time (p=0.0006; Appendix XIII), however, no clear seaonal pattern was apparent (Figure 30). Subsequently, when boring sponge damage was evaluated at each reef individually over time, no differences were observed (p>0.05; Appendix XIX).

Figure 30. Prevalence (%) of reef particles that were oyster shell and particles that exhibited evidence of boring sponge (*Cliona* spp.) damage. Means (+SE) are pooled for all reefs for each sample date. For each sample date n=24 and n=36 for dates in 2003 and 2004, respectively.



Reef particle size, as estimated by one-sided surface area (mm^2), varied significantly with *sample date, reef* and *date* x *reef* interaction (Appendix XX). However, changes over time were a direct function of where samples were taken within individual reefs. For example, some reef mounds were uncapped with oyster shell. When these mounds were sampled, much smaller sized surf clam particles were encountered and therefore significantly smaller means were calculated. Because these effects were not related to particle size change over time, but simply variation within reefs, we chose to pool data for each reef by all sample dates and analyze in a one-way ANOVA to better elucidate differences between reefs (Appendix XX). Subsequently, significant differences were seen between reefs ($p<0.0001$). Crane's Creek reef had the largest reef particles with Drumming Ground having the smallest (Table 13). Crane's

Table 13. Mean (SE) one-sided surface area (mm^2) of individual reef particles. Means with different letters were significantly different. Reef means are pooled for all sample dates for each reef. Quadrate sample size for each reef was 30. In the table, "n" refers to the total number of individual particles measured.

Reef[a]	n	Mean	(SE)
CC	513	2070	$(82)^{A}$
SB	652	1668	$(68)^{B}$
PR	724	1545	$(68)^{B,C}$
BP	761	1365	$(62)^{C}$
PB	1623	698	$(32)^{D}$
DG	2838	544	$(12)^{E}$

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Creek, Shell Bar, Parrot's Rock and Burton's Point reefs also exhibited a broader distribution of larger reef particles (Figure 31).

Because of the confounding factor of uncapped mounds being sampled at some reefs (other reefs contained no such mounds), we did not evaluate elevational differences in particle size in subsequent sections.

Correlation Analyses

Correlational analyses were performed on data pooled over the entire course of the study for each individual reef (n=6). Correlation coefficients were calculated between live oyster abundance and biomass ($\# \bullet m^{-2}$ and $g \bullet m^{-2}$) and oyster settlement, oyster disease prevalence, selected community metrics and physical reef descriptors (Table 14). The only significant correlation (negative) observed was between oyster biomass and reef crest depth

Figure 31. Size frequency distribution of surface area (mm^2) for individual reef particles during the course of the study at reefs in (A) Great Wicomico River, (B) Piankatank River and (C) Rappahannock River. The % frequency of particles are reported on the vertical axis. Values are aggregated in 200 mm^2 intervals. Thirty quadrate samples are pooled for each reef (see Table 13 for actual number of oyster measurements comprising each distribution).

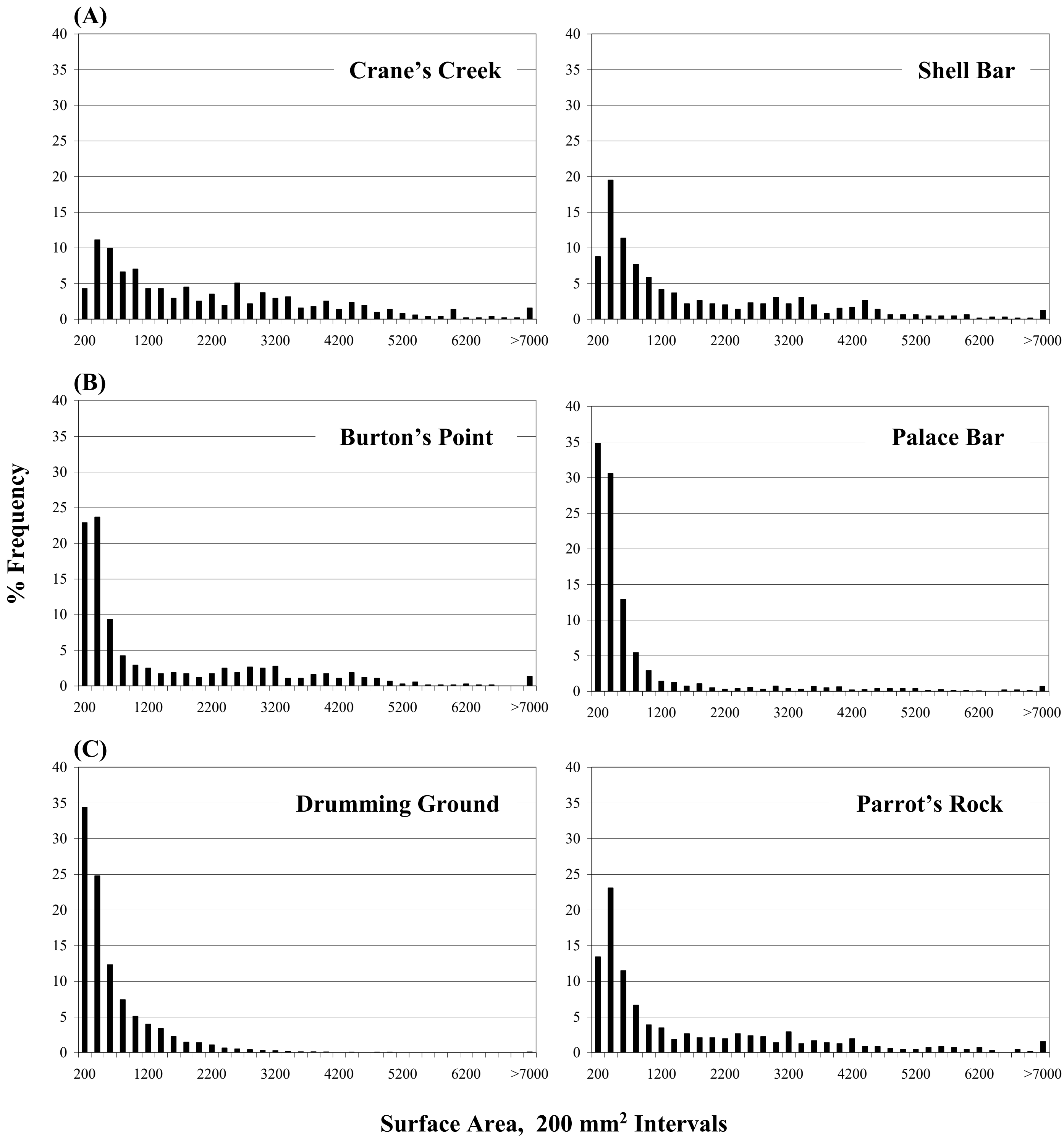


Table 14. Correlations between oyster abundance (# • m^{-2} and g • m^{-2}) and (A) oyster settlement and epifaunal metrics[a] and (B) disease[b] and reef architecture[c] parameters for reefs in this study. "r"=Pearson product moment coefficients and "p"= prob of r=0. Data are pooled for all sample dates in this analysis (n=6).

(A)

		Epifaunal Metrics				
Oyster Parameter	**Oyster Settlement**	**Non-oyster Abundance (# • m^{-2})**	**G. demissa**	**Non-M.t. % Cover**	**M.t. % Cover**	**Barnacle % Cover**
Density: # • m^{-2}						
r	-0.441	-0.235	-0.118	0.706	-0.647	0.794
p	0.38	0.653	0.824	0.117	0.164	0.059
Biomass: g • m^{-2}						
r	0.086	-0.086	0.200	0.714	-0.086	0.600
p	0.872	0.872	0.704	0.111	0.872	0.208

(B)

		Reef Architecture Metrics		
Oyster Parameter	**Disease Prevalence**	**Particle Surface Area (mm^2)**	**Crest Depth (m)**	**Reef Slope (%)**
Density: # • m^{-2}				
r	0.552	-0.294	-0.588	0.015
p	0.256	0.571	0.219	0.978
Biomass: g • m^{-2}				
r	0.086	0.314	**-0.886**	0.435
p	0.870	0.544	**0.019**	0.389

[a]See results section for detailed description of epifaunal metrics
[b]Prevalence of Dermo (Perkinsus marinus) from Fall 2003 and 2004 averaged
[c]See results section for detailed description of reef architecture metrics

(p=0.019). In addition, barnacle % cover was nearly significantly correlated (positively) with oyster abundance (p=0.059). It is important to note here that while a large number of samples and individual organisms were part of these analyses, the correlations were conducted using means for each individual reef and thus the tests for significance had relatively low power (df=5).

Preliminary Evidence of Elevational Stratification

Although reef community populations are often patchy, the original design for this study did not pose specific questions regarding elevational differences (e.g. reef crests vs. bases) within reefs for any of the parameters sampled. We did however sample from reef crests and flanks in 2003 in an effort to cover any intrinsic variation within reefs. These samples suggested that oyster density might have varied to a greater extent with elevation across these reefs than we had anticipated. Therefore in 2004, we chose to sample from crests, flanks and bases (see Figure 3). We decided to perform an *a posteriori* analysis to elucidate any patterns and added two components to data collection in 2004: quadrates along elevational transects and a small experiment to preliminarily evaluate substrate movement on reefs.

Initially, data were pooled over the entire study for each individual reef for crest and flank elevations only (since no base samples were collected in 2003) and one-way ANOVA performed on ranked live oyster and "box" oyster data (Kruskal-Wallis method) for each reef with *elevation* as the effect (Appendix XXI). Shell Bar reef had significantly more live oysters on flanks than crests (p=0.0177), but no differences were observed on other reefs for live or "box" oyster abundance (Table 15).

Table 15. Elevational differences in mean (SE) live oyster and "box" abundance (# • m^{-2}) within reefs for (A) data pooled over both years for crest and flank elevations only and (B) pooled data from 2004 only for all three elevations.

(A)

Reef	Elevation	Live C.v.	"Box" C.v.
Crane's Creek	Crest	79 (25)^{NS}	13 (6)^{NS}
	Flank	41 (14)	19 (8)
Shell Bar	Crest	**56 (17)***	19 (7)^{NS}
	Flank	**157 (30)**	40 (11)
Burton's Point	Crest	99 (45)^{NS}	16 (6)^{NS}
	Flank	48 (19)	11 (5)
Palace Bar	Crest	76 (34)^{NS}	13 (9)^{NS}
	Flank	141 (58)	8 (3)
Drumming Ground	Crest	11 (6)^{NS}	1 (1)^{NS}
	Flank	67 (34)	15 (8)
Parrot's Rock	Crest	112 (37)^{NS}	9 (5)^{NS}
	Flank	105 (45)	4 (3)

(B)

Reef	Elevation	Live C.v.	"Box" C.v.
Crane's Creek	Crest	35 (26)^{NS}	3 (3)^{NS}
	Flank	19 (13)	3 (3)
	Base	35 (20)	13 (9)
Shell Bar	Crest	**24 (11)***	11 (7)^{NS}
	Flank	**117 (31)**	27 (9)
	Base	**115 (17)**	43 (13)
Burton's Point	Crest	21 (18)^{NS}	0 (0)^{NS}
	Flank	3 (3)	0 (0)
	Base	21 (14)	3 (3)
Palace Bar	Crest	56 (41)^{NS}	0 (0)^{NS}
	Flank	37 (18)	8 (4)
	Base	128 (42)	24 (13)
Drumming Ground	Crest	**16 (10)****	**3 (3)****
	Flank	**8 (4)**	**3 (3)**
	Base	**160 (61)**	**83 (28)**
Parrot's Rock	Crest	53 (41)^{NS}	**3 (3)****
	Flank	45 (30)	**5 (5)**
	Base	104 (35)	**40 (12)**

^{NS} indicates means were not significantly different, p>0.05, between elevations
* indicates means were significantly different, p<0.05, between elevations
** indicates means were significantly different, p<0.01, between elevations

Data from 2004 only was then analyzed with all 3 reef elevations included in the model for each reef (Appendix XXI). Significant differences of live oyster abundance were observed at Drumming Ground ($p=0.0015$) and Shell Bar reefs ($p=0.0224$). Significant differences of "box" oyster abundance were observed at Drumming Ground ($p=0.0015$) and Parrot's Rock reefs ($p=0.0224$). In all of these cases, significantly higher abundances were found on reef bases than crests (Table 15).

Since oyster abundances differed most between the elevations sampled in 2004 (which included the significantly different bases), we limited all further analyses of elevational differences to the 2004 data. Significant differences (parametric two-way ANOVA with *reef* and *elevation* as main effects; Appendix XXII) in oyster shell height ($p=0.0002$) were observed between elevations (Table 16). The only significant difference observed for other epifaunal metrics was for total % cover of epifauna and barnacle % cover at Drumming Ground reef, while none were seen for other community parameters or other reefs (Kruskal-Wallis tests; Table 17 & Appendix XXIII). The % of oyster shell particles showed no differences between elevations; however, Drumming Ground reef had significantly ($p=0.0010$) more base particles with boring sponge damage (x=78.7%, se=10.3%) than other elevations (flank-x=26.7, SE=8.0; crest-x=16.6, SE=4.4), which were equal (Table 18).

Table 16. Elevational[a] differences in mean (SE) live oyster shell height (mm) within reefs for data pooled from 2004 only for all three elevations. Means labeled with different letters were significantly different.

Elevation	Shell Ht.**		
	n	Mean (SE)	
Crest	81	51.1	(1.5)[B]
Flank	101	57.2	(1.8)[A]
Base	228	58.8	(1.1)[A]

[a] See figure 3 for details on elevational locations
** indicates means were significantly different, $p<0.01$, between elevations

Table 17. Kruskal-Wallis p-values for each reef for the effect of *Elevation* on (A) abundance of non-oyster epifauna (# • m^{-2}), (B) ribbed mussel (*G. demissa*) abundance (# • m^{-2}) , (C) % cover of non-oyster epifauna, (D) % cover of barnacles (*Balanus* spp.) and (E) % cover of white crust (*M. tenuis*). Data for 2004 only for all three elevations. See Table 2 for taxa included in abundance and % cover groupings.

Reef	p-values				
	(A)	(B)	(C)	(D)	(E)
CC	0.8651	0.5969	0.8651	0.7339	0.6364
SB	0.3857	0.3857	0.1124	0.2052	0.1036
BP	0.3419	0.6163	0.6649	0.6804	0.3345
PB	0.1835	0.1187	0.5626	0.2824	0.6331
DG	0.1728	0.0791	**0.0301**	**0.0038**	0.5328
PR	0.6129	0.6129	0.4792	0.7326	0.2049

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Table 18. Kruskal-Wallis p-values for each reef for the effect of *Elevation* on prevalence (%) of oyster shell reef particles and particles exhibiting boring sponge (*Cliona* spp.) damage and the mean one-sided surface area of individual particles. Data for 2004 only for all three elevations.

Reef	p-values	
	% Oyster Shell	% *Cliona* spp.
CC	0.5302	0.5770
SB	0.6305	0.0669
BP	0.9199	0.5117
PB	0.7190	0.5802
DG	0.8026	**0.0010**
PR	0.9531	0.1499

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Transect quadrates – Quadrate samples were collected along three replicate transects every two meters from reef crest to the reef/seabed interface at Shell Bar and Palace Bar reefs in July and October of 2004, in order to provide more information on potential elevational differences in oyster abundance and size. Only oysters were enumerated in these samples (Appendices XXIV and XXV). Because the distance from crest to seabed varied within reefs, the distance along transects was standardized as a proportion with the crest=0 and the reef/seabed interface=1. While not rigorous like the previous analysis of oyster densities (both in terms of sample size and replication), a pattern of high variability emerged that emphasizes the patchiness of oyster populations on study reefs (Figure 32).

Shell Movement Experiment – One hundred and fifty-three of 192 painted shells were recovered after being deployed for 20 days. This period included a several day weather event having >40 knot northeasterly winds. The numbers of recovered shells and those flipped are reported in Appendix XXVI. We calculated the % movement of shells (which included the number flipped at least once and those gone from the deployment area) as an index of shell movement. Crane's Creek, Burton's Point and Parrot Rock had the largest amount of movement of shells deployed on the reef crests (Table 19). Shell movement was higher (n=4) or similar (n=1) on crests relative to flanks at all reefs except Drumming Ground (Table 19). It is important to note that statistical comparisons are inappropriate for this small experiment and, as such, any conclusions are qualitative.

Figure 32. Abundance of oysters (# • m^{-2}) collected in transect quadrates at (A) Shell Bar reef and (B) Palace Bar reef. Three transects were sampled at each reef for summer and fall 2004. The y-axis is the proportional distance from crest (0) to reef/seabed interface (1) of individual quadrate samples within a transect.

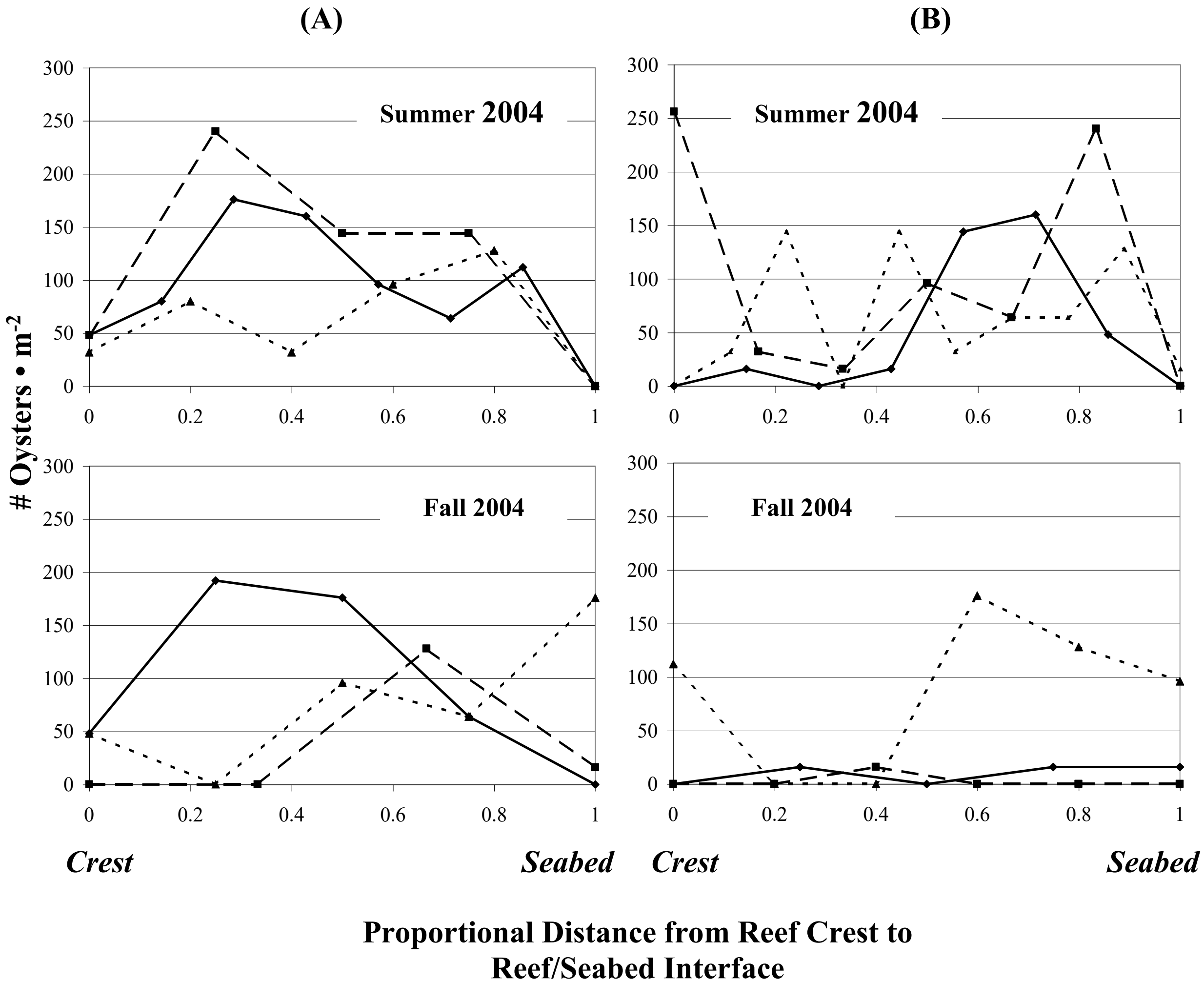


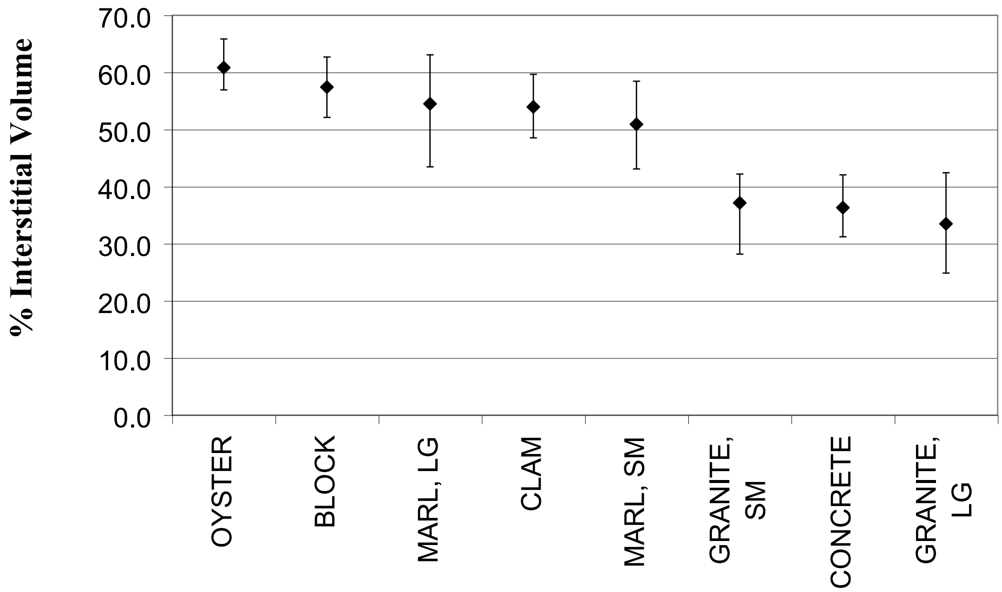
Table 19. Movement of painted shells deployed on crests and flanks of study reefs. Percent movement refers to the proportion of deployed shells that either flipped at least once or moved from the original location (Appendix XXVII contains specific data for this experiment). See figure 3 for details on elevations.

Reef	**% Movement**	
	Crest	**Flank**
Crane's Creek	81.3	87.5
Shell Bar	56.3	31.3
Burton's Point	93.8	56.3
Palace Bar	62.5	25.0
Drumming Ground	18.8	56.3
Parrot's Rock	100	37.5

Alternative Substrate Experiment

We deployed and retrieved 10 replicates baskets of each of eight substrate/size combinations (Table 3), weighing a total of approximately 15 tons, at the Palace Bar Reef in the Piankatank River. These substrates provided varying amount of interstitial space (Fig. 33) and differed in their surface rugosity. Unfortunately, the complete failure of recruitment to this reef during both 2003 and the exceedingly low recruitment in 2004 (Fig. 27) prevented us from meeting our objective here of evaluating the effectiveness of these substrates for reef restoration. A few individual oyster recruits were observed on some of the substrates in 2004, but there were insufficient numbers to warrant sorting through the tons of material. No data are reported for this portion of the study.

Figure 33. Interstitial volume (%) for the various materials being studied. Data points are mean (+/- min and max values)



DISCUSSION

Our monitoring of oyster reef restoration efforts was driven by some basic questions: *Is it working? If not, why? What can we do to improve our success?* There is clearly the widespread perception that if native oyster reef restoration is working, then we should, in the span of a few years, see a reversal in the decline of oyster standing stocks and fisheries landings in Virginia. Despite the expenditure of considerable funds over the past decade on oyster restoration in Virginia, there has not been a widespread recovery of oyster populations and there is a growing perception that native oyster restoration has failed, and that it has done so largely because of disease mortality. This in turn has resulted in pressure to introduce a more disease tolerant non-native oyster species.

In this project we followed the development of six reefs of varying age in three tributaries in the mesohaline portion of the Chesapeake Bay over a two-year period. During that period there was a significant overall decline in oyster abundances on the reefs; however, this was accompanied by an increase in the average biomass of individual oysters and no net change in total oyster biomass pooled across all reefs. Considerable differences were observed between reefs with some reefs (Burton's Point and Palace Bar) experiencing very significant declines in oyster abundance and biomass and others (Shell Bar, Cranes Creek and Drumming Ground) remaining stable or experiencing moderate declines. None of the reefs, however, achieved the desired goal of positive oyster population growth and standing stocks of oysters remain well below levels that we would perceive as a constituting a healthy oyster reef. So, we must ask, *Why is restoration of these reefs not working?*

The widely held perception is that the protozoans *Perkinsus marinus* and *Haplosporidium nelsoni*, the causative agents of Dermo and MSX diseases, respectively, are the causes of this failure to rebuild healthy oyster reefs in the Chesapeake Bay. The findings from this monitoring study cannot answer all of the questions that we might pose about the causes of the continued decline in oysters, but they do shed light on several of the processes controlling oyster populations of these reefs. First, it does not appear that disease constitutes the major cause of the observed decline during the two years of this study. Several lines of evidence support this assertion. During this study the region experienced above average rainfall and each of the tributaries had below average salinities (Fig.2). This likely contributed to the near absence of *H. nelsoni* (only 1 oyster throughout the 2 years tested positive for this parasite) and the low to moderate intensity of infections of *P. marinus* (Table 8). Although the mean density and total numbers of oysters declined on four of the six reefs over the course of the study (Figure 15), total oyster biomass did not decline significantly on the reefs (Figure 18) and size frequency distributions (Figs. 19 – 24) reveal that the greatest declines in oyster abundance occurred among small size classes of oysters that generally do not experience significant mortality from *P. marinus*. Furthermore, if we compare the decline in mean oyster density from the spring through the fall on each reef in each year (Table 4A) with the number of "box" oysters observed on each reef in the fall of that year (Table 4B), we cannot account for the observed declines based upon disease or other factors that would leave dead oysters with still articulated shells (Table 20). Christmas et al. (1997) estimated that roughly 50% of boxes remain articulated for more than 2 years in the upper Chesapeake Bay and Jordan et al. (2002) and Jordan and Coakley (2004) argue that "box" oyster counts provide a reasonable

Table 20. Comparison between the changes in mean density of oysters on each reef between spring and fall in each year and the density of "box" oysters (as an indicator of disease mortality) in the fall of each year.

	2003		2004	
Reef	Δ Density Live oysters from Spring – Fall (#•m^{-2})	Density of "box" oysters in Fall sample (#•m^{-2})	Δ Density Live oysters from Spring – Fall (#•m^{-2})	Density of "box" oysters in Fall sample (#•m^{-2})
PB	-256	0	-88	0
BP	-84	32	-18	0
PR	-288	0	-27	19
DG	-12	36	-101	16
SB	-128	28	-8	40
CC	-92	20	+2	11

estimate of annual natural mortality rates. By natural mortality rates here they are referring to mortalities associated with factors such as disease, low dissolved oxygen and water quality that do not break or crush the shells such as crab or ray predation. For oysters in the year 2 age class, which were generally > 55 mm in shell height in the current study, we assume that the # "box" oysters • m^{-2} provides a reasonable approximation of disease mortality within the past 6 months. It is evident from Table 20 that there were seldom sufficient numbers of "box" oysters observed to account for the declines observed in oysters over the summer. Since most of the observed decline was in small oysters, we assume that predation was the primary source of mortality among oysters on these reefs. We have previously measured high rates of predation among small oysters on reefs in the Rappahannock River (Luckenbach and Ross 2003).

Our findings also suggest that some of the reduction in oyster densities on the reefs may be associated with the movement of the substrate and attached oysters along the reef slope. This movement, which likely results from waves and currents, may cause oyster mortality or may have simply moved oysters off the reefs and out of the range of our sampling design. Future monitoring programs on these and other high relief reefs should take care to account for re-distribution of oysters down slope on the reefs and expand the sampling area to include extensive regions around the bases of reefs.

Our results indicate that extremely low recruitment followed by nearly complete mortality of new recruits within the first few months after settlement was the primary cause for the declining oyster populations on these reefs. The arrays of ceramic tile panels that we placed on the reef surface and retrieved at biweekly and weekly intervals from May through November have previously been shown to provide reliable estimates of recruitment to the reef surface (Luckenbach and Ross 2003). Several of the reefs had virtually no recruitment during the two years of this study (Fig. 27). Only Shell Bar Reef in the Great Wicomico during 2003 had even a moderate level of recruitment (Fig. 27), with the total cumulative recruitment estimated at 2450 oysters $\bullet$ m^{-2} (Table 7). Crane's Creek Reef in the Great Wicomico and Burton's Point Reef in the Piankatank had very modest recruitment levels during 2003 and 2004, respectively (Fig. 27 and Table 7). We point out that the recruitment numbers reported here should not be compared to "spat" counts from standard fall oyster surveys conducted by VMRC and VIMS. Those surveys, generally conducted in October and November, count juvenile oyster that are several mm's to over a cm in shell height and thus reflect settlement to the reef followed by several months of post-settlement mortality. The recruits to our settlement tiles were generally no more than one week post-settlement and typically < 1 mm in shell height. Thus, these values closely reflect settlement onto the reef.

For those reefs that did have modest recruitment the timing of the settlement peaks is revealing. The earliest recruitment to any of these reefs occurred during early August 2004 at Shell Bar and Burton's Point reefs (Fig. 27). The largest recruitment events observed during this period were at Shell Bar and Cranes's Creek reefs in late August and early September 2003. This differs from the historical pattern of oyster settlement reported for Chesapeake Bay (Kennedy and Krantz,1982) and the long-term temporal pattern in this region (VIMS oyster spatfall reports 1974-1992, http://www.vims.edu/mollusc/publications/mepubamr.htm), where peak oyster recruitment generally occurs during the early summer and is often followed by moderate settlement throughout the summer and a minor recruitment peak in August or September. The complete lack of new recruits early in the summer indicates a major recruitment failure to all six reefs in the three tributaries during both years of this study. The potential causes of this failure will be discussed later in this section.

When recruitment did occur to the reefs, our data indicate that early post-settlement mortality was very high. For instance, note that the two largest settlement peaks were observed in the Great Wicomico River on plates deployed on Shell Bar Reef on Aug. 19 and retrieved on Aug. 27 and on plates deployed on Crane's Creek Reef on Aug. 27 and retrieved on Sept. 3, 2003 (Fig. 27A, Appendix IV). However, very few new recruits were observed in samples taken from the reef surface of Oct. 7, 2003 (Figs. 19 & 20: Fall 2003 panel; see Appendix III for sample date and replicate information). The reasons for these very low numbers of new recruits surviving on the reefs in October are not known, but several plausible explanations exist. First, it is possible that settlement onto the ceramic tile arrays did not provide a good indicator of settlement onto the reef surface. Silt and/or other organisms attached to the shell substrate may have reduced the settlement of oysters onto the reef surface relative to the plates. We cannot rule out the role of silt on the reef surface, but our diver observations qualitatively indicate an abundance of clean shell on both reefs. Ribbed mussels, barnacles and an encrusting bryozoan were among the epifaunal organisms found on these reefs (Table 9) and these organisms may have reduced the settlement of oysters onto the reef surface; however, we note that total % cover of the shell surface by epifaunal organisms was < 50% on these reefs (Table 9, Fig. 28) and adequate space for oyster settlement appeared to be available. Similarly, the boring sponge *Cliona* sp., which has been implicated in degradation of the shells used as reef substrate in some restoration projects in Virginia, was found in very low abundance on the Crane's Creek and Burton's Point reefs and absent from the other reefs (Table 9). Our observations, therefore, suggest that while settlement onto these reefs may have been reduced slightly relative to the ceramic tiles sufficient clean, unoccupied space was apparently available for oyster settlement.

High rates of early post-settlement mortality in oysters have been attributed to predation in previous studies in Chesapeake Bay. Newell et al. (1998) observed 98% mortality during the first three months after settlement of oysters in a Maryland tributary of Chesapeake Bay, and they attributed most of this mortality to predation by flatworms (*Stylochus* spp.). Mann and Evans (1998) used an estimate of 93% mortality from settlement to 8 mm in shell height in modeling oyster populations in the James River, Virginia. In an unpublished study conducted by our research group in the Rappahannock River, early post-settlement mortality of oysters settled onto various substrates ranged from 40.7% to 82.1% over a 45 day period.

Because variation in this mortality was related to the interstitial space and surface complexity of the substrate which can provide refuge from predators, we attributed much of this mortality to predation by mud crabs (Xanthidae). In the current study we did not quantify predator abundance on the reefs, but suspect that predation by both flatworms and crabs contributed to the observed mortality.

Our data on the mobility of oyster shells on the reefs also raise the possibility that some of the oysters recruiting the reef surface may have been transported down the reef slope and out of range of our sampling, especially in 2003 when we did not sample at the base of the reefs, but only the crests and flanks. Other possible causes of high early post-settlement mortality among oysters on these reefs include, low dissolved oxygen associated with algal blooms and the direct effects of harmful algal blooms. This region of the Bay has previously been reported to be impacted by blooms of dinoflagellates that may be harmful to juvenile oysters (Luckenbach et al. 1993), but observations of such blooms were not made during the course of this study.

The most striking aspect of our findings, however, is the virtual lack of recruitment at most of the reefs during the two years of this study. With the exception of the modest recruitment observed on the two reefs in the Great Wicomico in 2003 and the very modest recruitment to Burton's Point Reef in the Piankatank Reef in 2004, we observe almost no recruitment of oysters over the two year period. As mentioned previously, there was also a complete lack of recruitment during the usual peak recruitment period in early summer. During this study we did not collect data to determine whether or not this lack of recruitment is indicative of a lack of spawning, poor larval survival or poor retention of larvae in the vicinity of the reefs. However, quantitative plankton tows were collected as part of a different study in the Great Wicomico and Rappahannock Rivers in the vicinity of the reefs during the summer of 2004 and they reveal only low numbers of oyster larvae in the water column beginning in mid-July (M. Southworth et al. unpubl. data), suggesting a lack of spawning earlier in the year. The summers of 2003 and 2004 experienced above annual rainfall and lower salinity in these tributaries than the long-term mean (Fig. 2); the late spring and early summer were also cool and marked by several storm events. Data from the Chesapeake Bay Monitoring Program in the mainstem of the Bay in the vicinity of the three tributaries studied here shows cooler surface water temperatures in June 2003 and 2004, relative to the previous five years (http://www.chesapeakebay.net/dat/indes.htm). We believe that these various pieces of data point to a general lack of spawning by oysters in these tributaries during the early summer in 2003 and 2004, followed by very modest spawning events in the late summer.

An unfortunate consequence of this recruitment failure was our inability to evaluate the effectiveness of the alternative substrates in promoting post-settlement survival. Good evidence that habitat complexity, measured as interstitial volume or surface rugosity, can affect survival rates of juvenile oysters and have a profound effect on the development of oyster reefs exits (Luckenbach et al. 2000, *unpubl. data*; O'Beirn et al. 2000). The experiment we deployed here was to provide the most extensive test to date of varying habitat complexity on oyster survival, but this obviously cannot be evaluated in the absence of oyster recruitment to the substrates. The variable nature of recruitment together with our observations here that smaller size classes of oysters exhibit the highest rates of mortality—presumably due to predation—further emphasize the need for future evaluation of the role of substrate complexity in enhancing the survival of new recruits to reefs.

In summary, the answer to our first question, *Is oyster reef restoration working?* has to be, *Not well*, in the systems studied here. However, we need to take care not to be too hasty in writing off these reefs. The Palace Bar Reef has persisted since it was created in 1993 and there remain viable oyster populations on all of the reefs, despite two successive years of recruitment failure. A few successive years of higher recruitment to any of these reefs would dramatically change the population structure and our perception of their success. The value of this study lies in the answers it provides to the question, *Why is the restoration not working as well as we would hope?* In recent years, there has been a growing perception by resource managers and the general public that the oyster diseases Dermo and MSX are the overwhelming cause of the continuing decline in oyster stocks. It is clear for this study that recruitment failure, not massive disease mortality, was responsible for most of the decline oyster abundances on the reefs between 2003 and 2004. Diseases can, of course, be playing a role in this by reducing the spawning stock and thus leading to reduced reproductive output. However, it is clear from the population size structures observed on the reefs in 2003 and 2004 (Figs. 19-24) that moderate densities of spawning stocks existed on most of the reefs. There is little doubt that increasing these densities will be a crucial element in improving the success of our restoration efforts. Nevertheless, the nearly complete recruitment failure observed on most of the reefs during the two years of this study is not solely the result of low brood stock numbers and we have argued that climatic conditions played an important role in reduced spawning during this period. Our findings also point to a few things that we can do to improve our success in restoring reefs. The addition of brood stocks to the Shell Bar Reef in the Great Wicomico River appears to have enhanced the recruitment to it and to the Crane's Creek Reef. Restoration efforts in areas that are recruitment limited should employ brood stock enhancement—and we would argue for massive brood stock additions—for the purpose of increasing recruitment. As our findings make clear, however, we must still be prepared for years when recruitment failure may occur for other reasons and expect occasional declines in oyster abundance.

Natural mortality of oysters from processes other than disease, such as predation, physical transport and damage on unconsolidated reefs, and water quality need to be given greater consideration in our restoration efforts. We have shown that disease was not the major culprit in the declining abundances of oysters on these reefs between 2003 and 2004. We note here that there is no evidence that a disease-tolerant non-native oyster would have fared any better over this period. Developing better methods to deploy and protect brood stocks, improve early post-settlement survival and increase the stability of reef bases would likely be rewarded with increased success in our restoration efforts.

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LIST OF APPENDICES

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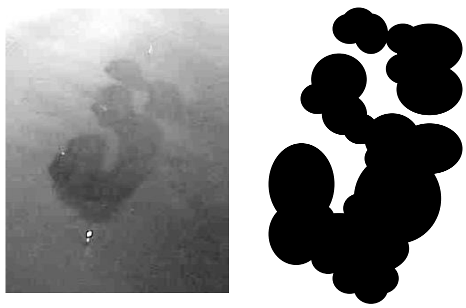
Appendix I. Latitude and longitude for study reefs.

Tributary	Reef	Lat. – Long.
Great Wicomico River	Crane's Creek	N 37° 48.521' W 076° 18.198'
	Shellbar	N 37° 49.739' W 076° 19.102'
Piankatank River	Burton's Point	N 37° 30.690' W 076° 19.936'
	Palace Bar	N 37° 31.693' W 076° 22.433'
Rappahannock River	Drumming Ground	N 37° 39.248' W 076° 27.648'
	Parrots Rock	N 37° 36.443' W 076° 25.412'

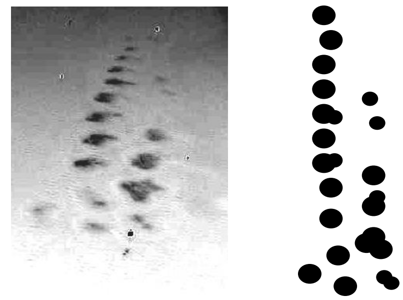
Appendix II. Digitally enhanced aerial photographs paired with aerial footprint schematics of individual shell mounds for each reef in this study.

A) Reefs in Great Wicomico River

Crane's Creek Reef

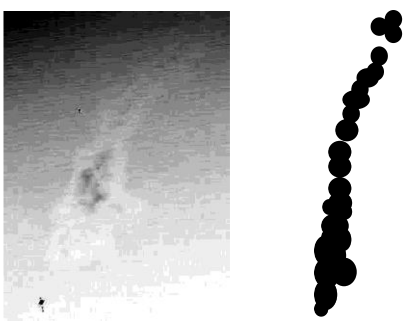


Shell Bar Reef

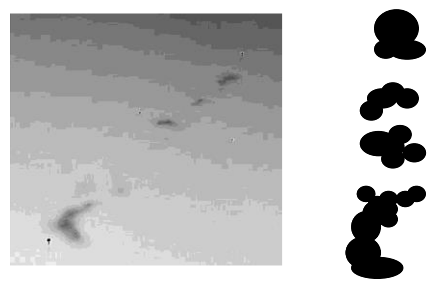


B) Reefs in Piankatank River

Burton's Point Reef

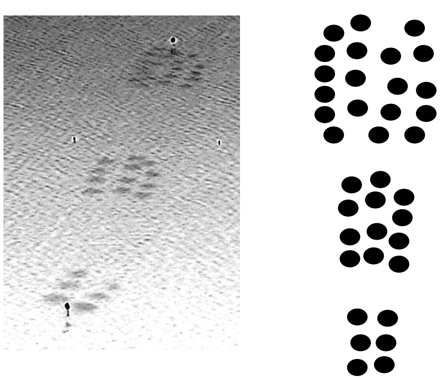


Palace Bar Reef

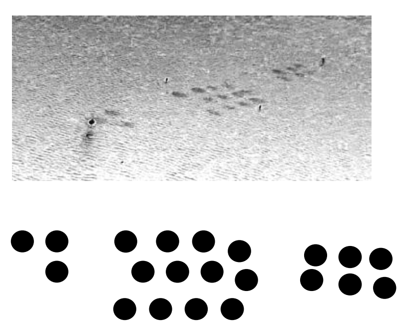


C) Reefs in Rappahannock River

Drumming Ground Reef



Parrot's Rock Reef



Appendix III – Dates and number of replicate samples collected at reefs in this study for (A) regular quadrate samples (all six reefs) and (B) transect quadrate samples (only two selected reefs). Note that a total of four replicate regular quadrates were collected at each reef during each season during 2003, while six were collected during 2004. Transect quadrates were only collected during summer and fall of 2004 at two reef sites (see appropriate methods and results sections for details).

Appendix 2. **Regular Quadrates-Total number collected during study=180**

Season	**Date**	**# per Elevation**		
		Crest	**Flank**	**Base**
Spring 2003	5/21 & 5/22	2	2	-
Summer 2003	7/15	2	2	-
Fall 2003	10/7	2	2	-
Spring 2004	5/24 & 5/25	2	2	2
Summer 2004	7/13 & 7/14	2	2	2
Fall 2004	10/4 & 10/5	2	2	2

(B) Transect Quadrates-Total number collected during study=75

Season	Date	**Reef**	**Transect #**	**Transect Length (m)**	**# of Quadrates**
Summer 2004	7/13	Shell Bar	1	14	8
			2	8	5
			3	10	6
	7/14	Palace Bar	1	14	8
			2	12	7
			3	18	10
Fall 2004	10/5	Shell Bar	1	8	5
			2	6	4
			3	8	5
	10/5	Palace Bar	1	8	5
			2	10	6
			3	10	6

Appendix IV. Dates and durations for deployment of tile arrays for oyster settlement during (A) 2003 and (B) 2004.

A) Summer 2003-Total number of tiles deployed=4,320

Deployment #	Date Deployed	Date Retrieved	# Days in Field
1	5/12	5/28	15
2	5/28	6/10	12
3	6/10	6/25	14
4	6/25	7/9	13
5	7/9	7/23	13
6	7/23	8/8	15
7	8/8	8/19	10
8	8/19	8/27	7
9	8/27	9/3	6
10	9/3	9/10	6
11	9/10	9/16	5
12	9/16	9/24	7
13	9/24	9/30	5
14[a]	9/30	10/15	14
15[b]	10/15	11/5	20

[a] Three reefs (DG, PB & BP; see Table 1 for abbreviations) retrieved 10/17 and were in the field for 16 days.
[b] Three reefs (DG, PB & BP) deployed 10/17 and were in the field for 18 days.

Appendix IV Continued

Appendix 2. **Summer 2004 –Total number of tiles deployed=4,032**

Deployment #	Date Deployed	Date Retrieved	# Days in Field
1[a]	5/24	6/8	14
2	6/8	6/22	13
3	6/22	7/6	13
4	7/6	7/21	14
5	7/21	7/28	6
6	7/28	8/4	6
7	8/4	8/11	6
8	8/11	8/17	5
9	8/17	8/24	6
10	8/24	8/31	6
11[b]	8/31	9/14	13
12[c]	9/14	9/27	12
13[d]	10/4	10/12	7
14	10/12		

[a] DG (see Table 1 for abbreviations) deployed 5/25 and retrieved 6/8 for 13 days in the field.
[b] PB & BP retrieved on 9/16 were in the field for 15 days.
[c] PB & BP deployed 9/16 and retrieved 9/27 for 10 days in the field.
[d] CC & SB deployed 10/5 and retrieved on 10/12 for 6 days in the field.

Appendix V. Density (# • m^{-2}) of live and "box" oysters collected in regular quadrate samples for each reef during each sample period. See Appendix III for number of replicate quadrates for each sample.

Date	River[a]	Reef Name[b]	Live		Box	
			Mean	SE	Mean	SE
SPRING 2003	GW	CC	128	49	28	10
	GW	SB	228	59	32	17
	PIANK	BP	188	119	40	8
	PIANK	PB	360	123	12	8
	RAPP	DG	104	88	4	4
	RAPP	PR	332	74	12	12
SUMMER 2003	GW	CC	116	18	40	15
	GW	SB	100	16	60	27
	PIANK	BP	112	33	8	5
	PIANK	PB	152	43	40	25
	RAPP	DG	0	0	0	0
	RAPP	PR	128	40	16	7
FALL 2003	GW	CC	36	31	20	15
	GW	SB	100	40	28	18
	PIANK	BP	104	44	32	9
	PIANK	PB	0	0	0	0
	RAPP	DG	92	56	36	21
	RAPP	PR	44	44	0	0
SPRING 2004	GW	CC	27	13	8	8
	GW	SB	80	30	24	14
	PIANK	BP	21	14	0	0
	PIANK	PB	107	36	13	6
	RAPP	DG	125	69	56	33
	RAPP	PR	64	40	8	5
SUMMER 2004	GW	CC	32	26	0	0
	GW	SB	104	23	16	7
	PIANK	BP	21	18	3	3
	PIANK	PB	96	49	19	13
	RAPP	DG	35	25	16	10
	RAPP	PR	101	43	21	13
FALL 2004	GW	CC	29	20	11	5
	GW	SB	72	31	40	11
	PIANK	BP	3	3	0	0
	PIANK	PB	19	10	0	0
	RAPP	DG	24	14	16	16
	RAPP	PR	37	17	19	12

Appendix VI. Analysis of the effects of *Sample Date* and *Reef* on (A) # live oysters • m^{-2}, (B) # "box" oysters • m^{-2} and (C) oyster ash-free dry tissue biomass (g) • m^{-2} using Friedman's method by performing main-effects two-way ANOVA on data ranked within each date.

(A)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	1555	311	4.11	**0.0015**
Reef	5	1331	266	3.51	**0.0048**

(B)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	1555	311	5.08	**0.0002**
Reef	5	847	169	2.77	**0.0199**

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Source	DF	Type III SS	Mean Square	F-value	p
Date	5	194	39	1.98	0.0913
Reef	5	318	64	3.23	**0.0105**

Appendix VII. Ash-free dry tissue biomass (mg) of individual oysters and area standardized oyster ash-free dry tissue biomass (g • m^{-2}) collected in regular quadrate samples for each reef during each sample period. See Appendix III for number of replicate quadrates for each sample. Below, "n" refers to the number of individuals measured within each grouping.

Date	River[a]	Reef Name[b]	Individual Biomass			Biomass per Reef Area	
			n	Mean	SE	Mean	SE
SPRING 2003	GW	CC	32	237.1	37.9	30.4	15.8
	GW	SB	67	595.4	85.5	159.6	132.6
	PIANK	BP	47	218.5	48.6	41.1	17.3
	PIANK	PB	90	298.0	38.7	107.3	42.7
	RAPP	DG	26	197.2	28.9	20.5	17.3
	RAPP	PR	83	216.4	17.4	71.9	4.1
SUMMER 2003	GW	CC	29	410.0	61.6	47.6	14.0
	GW	SB	25	723.6	144.9	72.4	56.5
	PIANK	BP	28	399.4	70.3	44.7	1.3
	PIANK	PB	38	478.2	127.9	72.7	40.8
	RAPP	DG	0	0.0	0.0	0.0	0.0
	RAPP	PR	32	439.2	44.5	56.2	19.8
FALL 2003	GW	CC	9	473.8	155.2	17.1	4.9
	GW	SB	25	317.6	50.9	31.8	6.9
	PIANK	BP	26	385.2	34.2	40.1	10.3
	PIANK	PB	0	0.0	0.0	0.0	0.0
	RAPP	DG	23	400.9	45.3	36.9	36.9
	RAPP	PR	11	679.6	100.6	29.9	29.9
SPRING 2004	GW	CC	9	568.2	217.9	13.6	9.8
	GW	SB	30	648.7	87.6	51.9	30.5
	PIANK	BP	8	640.3	110.6	13.7	13.7
	PIANK	PB	40	766.7	94.0	81.8	45.3
	RAPP	DG	47	561.9	39.7	70.4	63.4
	RAPP	PR	24	612.5	53.2	39.2	25.8
SUMMER 2004	GW	CC	12	423.5	72.5	13.6	9.6
	GW	SB	39	727.8	70.5	75.7	22.4
	PIANK	BP	8	498.0	61.9	10.6	10.1
	PIANK	PB	36	822.4	95.7	78.9	36.4
	RAPP	DG	13	605.2	101.2	21.0	17.0
	RAPP	PR	38	975.5	75.6	98.8	62.3
FALL 2004	GW	CC	38	814.9	71.6	82.6	36.4
	GW	SB	27	796.0	82.0	57.3	22.8
	PIANK	BP	1	317.2	.	0.8	0.8
	PIANK	PB	7	618.3	149.2	11.5	8.1
	RAPP	DG	10	492.6	138.3	13.1	13.1
	RAPP	PR	14	791.3	161.7	29.5	11.1

[a]GW=Great Wicomico; PIANK=Piankatank; RAPP=Rappahannock
[b]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Appendix VIII. Shell height (mm) of live and "box" oysters collected in regular quadrate samples for each reef during each sample period. See Appendix III for number of replicate quadrates for each sample. Below, "n" refers to the number of individuals measured within each grouping.

Date	River[a]	Reef Name[b]	Shell Height Live			Shell Height Box		
			n	Mean	SE	n	Mean	SE
SPRING 2003	GW	CC	32	33.6	2.6	7	42.3	3.5
	GW	SB	67	46.7	3.2	8	56.5	8.1
	PIANK	BP	47	31.5	2.2	10	38.5	5.6
	PIANK	PB	90	37.5	1.5	3	42.3	14.2
	RAPP	DG	26	32.1	2.2	1	31.0	.
	RAPP	PR	83	33.6	1.2	3	40.6	1.9
SUMMER 2003	GW	CC	39	44.1	2.8	10	47.1	4.6
	GW	SB	40	54.2	4.6	15	43.1	4.2
	PIANK	BP	31	43.0	3.0	2	41.8	9.7
	PIANK	PB	45	44.7	3.2	10	34.8	2.3
	RAPP	DG	0	.	.	0	.	.
	RAPP	PR	36	46.7	2.1	4	46.2	8.5
FALL 2003	GW	CC	9	43.7	7.7	1	29.8	.
	GW	SB	25	38.5	3.1	7	43.9	4.4
	PIANK	BP	26	44.9	1.7	8	47.2	2.3
	PIANK	PB	0	.	.	0	.	.
	RAPP	DG	23	44.8	2.5	9	34.0	3.2
	RAPP	PR	11	57.1	3.6	0	.	.
SPRING 2004	GW	CC	9	46.3	8.7	4	50.6	2.7
	GW	SB	30	54.4	2.9	9	78.7	13.4
	PIANK	BP	8	55.3	4.7	0	.	.
	PIANK	PB	40	58.2	2.8	5	66.1	16.8
	RAPP	DG	47	52.5	1.6	21	44.1	2.5
	RAPP	PR	24	54.8	2.1	3	67.1	7.4
SUMMER 2004	GW	CC	12	46.1	3.4	0	.	.
	GW	SB	39	57.0	2.8	6	47.2	9.2
	PIANK	BP	9	50.3	3.4	1	47.5	.
	PIANK	PB	38	61.2	2.5	7	70.9	7.2
	RAPP	DG	13	53.4	4.1	7	43.5	6.8
	RAPP	PR	38	66.7	2.2	8	56.4	2.8
FALL 2004	GW	CC	38	60.7	2.6	19	44.2	2.7
	GW	SB	27	60.6	2.7	15	44.5	2.5
	PIANK	BP	1	42.3	.	0	.	.
	PIANK	PB	7	51.9	7.9	0	.	.
	RAPP	DG	10	46.5	6.2	5	52.7	6.6
	RAPP	PR	14	56.3	6.7	7	61.8	5.5

[a]GW=Great Wicomico; PIANK=Piankatank; RAPP=Rappahannock

[b]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Appendix IX. Two-way ANOVA of the effects of *Sample Date* and *Reef* on (A) live oyster shell height (mm), (B) "box" oyster shell height and (C) individual live oyster ash-free dry tissue biomass (mg).

(A)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	44535	8907	34.40	**<0.0001**
Reef	5	5895	1179	4.55	**0.0004**
Date x Reef	23	17458	759	2.93	**<0.0001**

(B)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	6631	1326	4.76	**0.0004**
Reef	5	3065	613	2.20	**0.0532**
Date x Reef	18	10482	582	2.09	**0.0077**

(C)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	16213484	3242697	17.03	**<0.0001**
Reef	5	3993754	798751	4.20	**0.0009**
Date x Reef	23	11435747	497206	2.61	**<0.0001**

Appendix X. Area and time standardized oyster settlement (# oysters • m^{-2} • $week^{-1}$) for reefs in the Great Wicomico River over the entire course of the study. See Appendix IV for number of replicate settlement gear and length of deployment for each sample.

Reef	Date	Mean	SE	Reef	Date	Mean	SE
Crane's Creek	5/28/2003	0.00	0.00	**Shell Bar**	5/28/2003	0.00	0.00
	6/10/2003	0.00	0.00		6/10/2003	0.00	0.00
	6/25/2003	0.00	0.00		6/25/2003	0.00	0.00
	7/9/2003	0.00	0.00		7/9/2003	0.00	0.00
	7/23/2003	0.00	0.00		7/23/2003	0.00	0.00
	8/8/2003	0.00	0.00		8/8/2003	0.00	0.00
	8/19/2003	16.78	5.19		8/19/2003	117.68	8.09
	8/27/2003	50.68	15.39		8/27/2003	1431.60	202.81
	9/3/2003	405.68	117.36		9/3/2003	851.98	90.33
	9/10/2003	30.05	11.16		9/10/2003	30.93	15.81
	9/16/2003	10.23	4.19		9/16/2003	8.98	5.48
	9/24/2003	0.00	0.00		9/24/2003	1.83	1.83
	9/30/2003	0.00	0.00		9/30/2003	2.80	2.80
	10/15/2003	5.50	3.18		10/15/2003	4.15	1.52
	11/5/2003	0.00	0.00		11/5/2003	0.00	0.00
	6/8/2004	0.00	0.00		6/8/2004	0.00	0.00
	6/22/2004	0.00	0.00		6/22/2004	0.00	0.00
	7/6/2004	0.00	0.00		7/6/2004	0.00	0.00
	7/21/2004	0.00	0.00		7/21/2004	1.83	1.83
	7/28/2004	0.00	0.00		7/28/2004	0.00	0.00
	8/4/2004	0.00	0.00		8/4/2004	33.25	16.10
	8/11/2004	0.00	0.00		8/11/2004	0.00	0.00
	8/17/2004	0.00	0.00		8/17/2004	2.55	2.55
	8/24/2004	0.00	0.00		8/24/2004	0.00	0.00
	8/31/2004	0.00	0.00		8/31/2004	0.00	0.00
	9/14/2004	0.00	0.00		9/14/2004	0.00	0.00
	9/27/2004	1.08	1.08		9/27/2004	5.73	4.41
	10/12/2004	0.00	0.00		10/12/2004	0.00	0.00
	11/3/2004	0.00	0.00		11/3/2004	0.00	0.00

Appendix XI. Area and time standardized oyster settlement (# oysters • m^{-2} • $week^{-1}$) for reefs in the Piankatank River over the entire course of the study. See Appendix IV for number of replicate settlement gear and length of deployment for each sample.

Reef	Date	Mean	SE	Reef	Date	Mean	SE
Burton's Point	5/28/2003	0.00	0.00	Palace Bar	5/28/2003	0.00	0.00
	6/10/2003	0.00	0.00		6/10/2003	0.00	0.00
	6/25/2003	0.00	0.00		6/25/2003	0.00	0.00
	7/9/2003	0.00	0.00		7/9/2003	0.00	0.00
	7/23/2003	0.00	0.00		7/23/2003	0.00	0.00
	8/8/2003	0.00	0.00		8/8/2003	0.85	0.85
	8/19/2003	0.00	0.00		8/19/2003	0.00	0.00
	8/27/2003	0.00	0.00		8/27/2003	0.00	0.00
	9/3/2003	0.00	0.00		9/3/2003	0.00	0.00
	9/10/2003	0.00	0.00		9/10/2003	0.00	0.00
	9/16/2003	2.55	2.55		9/16/2003	0.00	0.00
	9/24/2003	0.00	0.00		9/24/2003	0.00	0.00
	9/30/2003	0.00	0.00		9/30/2003	0.00	0.00
	10/17/2003	0.88	0.88		10/17/2003	0.00	0.00
	11/5/2003	0.00	0.00		11/5/2003	0.00	0.00
	6/8/2004	0.00	0.00		6/8/2004	0.00	0.00
	6/22/2004	0.00	0.00		6/22/2004	0.00	0.00
	7/6/2004	0.00	0.00		7/6/2004	0.00	0.00
	7/21/2004	0.00	0.00		7/21/2004	0.00	0.00
	7/28/2004	0.00	0.00		7/28/2004	0.00	0.00
	8/4/2004	89.58	37.75		8/4/2004	0.00	0.00
	8/11/2004	0.00	0.00		8/11/2004	0.00	0.00
	8/17/2004	0.00	0.00		8/17/2004	0.00	0.00
	8/24/2004	0.00	0.00		8/24/2004	0.00	0.00
	8/31/2004	0.00	0.00		8/31/2004	0.00	0.00
	9/16/2004	0.00	0.00		9/16/2004	0.00	0.00
	9/27/2004	1.28	1.28		9/27/2004	16.63	16.63
	10/12/2004	0.00	0.00		10/12/2004	0.00	0.00
	11/3/2004	0.00	0.00		11/3/2004	0.00	0.00

Appendix XII. Area and time standardized oyster settlement (# oysters • m^{-2} • $week^{-1}$) for reefs in the Rappahannock River over the entire course of the study. See Appendix IV for number of replicate settlement gear and length of deployment for each sample.

Reef	Date	Mean	SE	Reef	Date	Mean	SE
Drumming Ground	5/28/2003	0.00	0.00	**Parrot's Rock**	5/28/2003	0.00	0.00
	6/10/2003	0.00	0.00		6/10/2003	0.00	0.00
	6/25/2003	0.00	0.00		6/25/2003	0.00	0.00
	7/9/2003	0.00	0.00		7/9/2003	0.00	0.00
	7/23/2003	0.00	0.00		7/23/2003	0.00	0.00
	8/8/2003	0.00	0.00		8/8/2003	0.00	0.00
	8/19/2003	0.00	0.00		8/19/2003	0.00	0.00
	8/27/2003	1.83	1.83		8/27/2003	0.00	0.00
	9/3/2003	17.48	0.38		9/3/2003	0.00	0.00
	9/10/2003	0.00	0.00		9/10/2003	0.00	0.00
	9/16/2003	0.00	0.00		9/16/2003	0.00	0.00
	9/24/2003	0.00	0.00		9/24/2003	0.00	0.00
	9/30/2003	0.00	0.00		9/30/2003	0.00	0.00
	10/17/2003	0.00	0.00		10/15/2003	0.00	0.00
	11/5/2003	0.00	0.00		11/5/2003	0.00	0.00
	6/8/2004	0.00	0.00		6/8/2004	0.00	0.00
	6/22/2004	0.00	0.00		6/22/2004	0.00	0.00
	7/6/2004	0.00	0.00		7/6/2004	0.00	0.00
	7/21/2004	0.00	0.00		7/21/2004	0.00	0.00
	7/28/2004	0.00	0.00		7/28/2004	0.00	0.00
	8/4/2004	0.00	0.00		8/4/2004	0.00	0.00
	8/11/2004	0.00	0.00		8/11/2004	0.00	0.00
	8/17/2004	0.00	0.00		8/17/2004	0.00	0.00
	8/24/2004	0.00	0.00		8/24/2004	0.00	0.00
	8/31/2004	0.00	0.00		8/31/2004	0.00	0.00
	9/14/2004	0.00	0.00		9/14/2004	0.00	0.00
	9/27/2004	4.58	3.30		9/27/2004	4.30	0.00
	10/12/2004	0.00	0.00		10/12/2004	0.00	0.00
	11/3/2004	0.00	0.00		11/3/2004	0.00	0.00

Appendix XIII. Kruskal-Wallis analysis of the effect of *Reef* on area and time standardized oyster settlement (# oysters • m^{-2} • $week^{-1}$) for (A) 2003 and (B) 2004.

(A)

Source	DF	Type III SS	Mean Square	F-value	p
Reef	5	1033824	206765	18.07	**<0.0001**

(B)

Source	DF	Type III SS	Mean Square	F-value	p
Reef	5	78266	15653	2.40	**0.0374**

Appendix XIV. Density (# • m^{-2}) of all non-oyster epibenthic organisms and ribbed mussels (*Guekinsia demissa*) collected in regular quadrate samples for each reef during each sample period. See Appendix III for number of replicate quadrates for each sample and Table 2 for list of organisms included in this group.

Date	River[a]	Reef Name[b]	Non-Oyster Epibenthos		*G. demissa*	
			Mean	SE	Mean	SE
SPRING 2003	GW	CC	308	224	308	224
	GW	SB	4	4	0	0
	PIANK	BP	10	8	0	0
	PIANK	PB	40	10	8	5
	RAPP	DG	30	14	24	14
	RAPP	PR	250	92	212	97
SUMMER 2003	GW	CC	484	163	484	163
	GW	SB	16	8	12	8
	PIANK	BP	14	14	8	15
	PIANK	PB	40	4	40	4
	RAPP	DG	20	12	20	12
	RAPP	PR	392	104	380	104
FALL 2003	GW	CC	276	238	276	238
	GW	SB	12	9	12	8
	PIANK	BP	24	9	20	5
	PIANK	PB	4	14	4	14
	RAPP	DG	12	12	12	12
	RAPP	PR	104	223	104	219
SPRING 2004	GW	CC	61	17	29	16
	GW	SB	0	0	0	0
	PIANK	BP	3	3	0	0
	PIANK	PB	125	81	101	76
	RAPP	DG	40	13	27	9
	RAPP	PR	133	127	131	124
SUMMER 2004	GW	CC	136	130	133	130
	GW	SB	13	8	13	8
	PIANK	BP	3	3	3	3
	PIANK	PB	69	40	61	42
	RAPP	DG	8	5	5	5
	RAPP	PR	48	39	48	39
FALL 2004	GW	CC	224	146	224	146
	GW	SB	0	0	0	0
	PIANK	BP	3	3	3	3
	PIANK	PB	21	10	8	5
	RAPP	DG	8	8	8	8
	RAPP	PR	11	8	11	8

[a]GW=Great Wicomico; PIANK=Piankatank; RAPP=Rappahannock
[b]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Appendix XV. Abundance (% cover) of total non-white crust epibenthic organisms, barnacles (*Balanus* spp.) and white crust (*Membranipora tenuis*) collected in regular quadrate samples for each reef during each sample period. See Appendix III for number of replicate quadrates and Table 2 for list of organisms included in this group.

Date	River[a]	Reef Name[b]	Total Non-*M. tenuis* Epibenthos		*Belanus* spp.		*M. tenuis*	
			Mean	SE	Mean	SE	Mean	SE
SPRING 2003	GW	CC	10	3	3	1	53	5
	GW	SB	5	1	1	0	48	8
	PIANK	BP	17	5	15	5	48	5
	PIANK	PB	9	6	8	6	15	9
	RAPP	DG	3	2	2	1	38	13
	RAPP	PR	49	4	45	5	18	10
SUMMER 2003	GW	CC	20	1	18	1	4	5
	GW	SB	24	5	23	4	9	8
	PIANK	BP	22	4	19	3	8	9
	PIANK	PB	15	1	14	1	9	1
	RAPP	DG	4	3	4	3	7	5
	RAPP	PR	31	2	28	1	6	0
FALL 2003	GW	CC	4	1	3	1	15	2
	GW	SB	17	7	16	6	33	6
	PIANK	BP	9	8	6	7	15	4
	PIANK	PB	2	6	2	6	2	5
	RAPP	DG	4	1	4	1	11	3
	RAPP	PR	2	5	2	4	0	2
SPRING 2004	GW	CC	5	2	3	2	19	4
	GW	SB	3	1	3	1	30	8
	PIANK	BP	6	2	5	2	14	4
	PIANK	PB	12	7	12	7	18	9
	RAPP	DG	9	5	8	6	14	6
	RAPP	PR	2	0	1	0	9	4
SUMMER 2004	GW	CC	2	0	1	0	20	6
	GW	SB	4	1	2	2	11	3
	PIANK	BP	2	0	1	0	2	1
	PIANK	PB	14	5	9	4	4	2
	RAPP	DG	3	2	2	2	5	3
	RAPP	PR	7	3	6	2	8	1
FALL 2004	GW	CC	16	1	6	1	31	7
	GW	SB	8	1	5	0	16	4
	PIANK	BP	4	1	4	1	8	1
	PIANK	PB	13	2	10	3	23	4
	RAPP	DG	4	1	3	1	11	3
	RAPP	PR	7	1	5	2	18	3

[a]GW=Great Wicomico; PIANK=Piankatank; RAPP=Rappahannock
[b]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Appendix XVI. Analysis of the effects of *Sample Date* and *Reef* on the density of (A) total non-oyster epibenthos (# • m^{-2}), (B) ribbed mussels (*G. demissa*; # • m^{-2}), (C) total non-white crust epibenthos (% cover), (D) barnacles (*Balanus* spp.; % cover) and (E) white crust (*M. tenuis*; % cover), using Friedman's method by performing main-effects two-way ANOVA on data ranked within each date.

(A)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	1555	311	5.48	**0.0001**
Reef	5	3029	606	10.68	**<0.0001**

(B)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	1555	311	5.63	**<0.0001**
Reef	5	2407	481	8.71	**<0.0001**

(C)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	1555	311	3.92	**0.0022**
Reef	5	2011	402	5.31	**0.0001**

(D)

Source	DF	Type III SS	Mean Square	F-value	P
Date	5	1477	295	3.93	**0.0022**
Reef	5	1073	215	2.85	**0.0169**

(E)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	1489	298	3.96	**0.0020**
Reef	5	1731	346	4.61	**0.0006**

Appendix XVII. Prevalence (%) of particles with evidence of boring sponge (*Cliona* spp.) damage and oyster shell particles and mean one-sided surface area (mm^2) of individual reef particles collected in regular quadrate samples for each reef during each sample period. See Appendix III for number of replicate quadrates for each sample.

Date	River[a]	Reef Name[b]	% Boring Sponge		% Oyster Shell		Surface Area (mm^2)	
			Mean	SE	Mean	SE	Mean	SE
SPRING 2003	GW	CC	100.0	0.0	100.0	0.0	2742	278
	GW	SB	81.9	9.0	97.2	2.8	2043	190
	PIANK	BP	74.0	9.7	94.1	2.4	1091	132
	PIANK	PB	54.9	16.6	70.9	23.6	448	37
	RAPP	DG	31.0	14.3	85.0	14.7	401	16
	RAPP	PR	74.9	7.4	92.6	4.3	1463	119
SUMMER 2003	GW	CC	87.1	4.5	100.0	0.0	1749	196
	GW	SB	72.2	7.5	100.0	0.0	1650	180
	PIANK	BP	91.7	8.3	99.4	0.7	1430	203
	PIANK	PB	79.1	7.5	99.0	1.0	867	116
	RAPP	DG	8.0	2.1	84.3	15.8	592	33
	RAPP	PR	61.8	4.6	95.5	3.0	1615	199
FALL 2003	GW	CC	91.1	3.6	100.0	0.0	2186	254
	GW	SB	90.0	4.1	100.0	0.0	3007	347
	PIANK	BP	88.4	3.6	100.0	0.0	3254	312
	PIANK	PB	91.4	4.2	100.0	0.0	3852	433
	RAPP	DG	52.2	9.8	100.0	0.0	1112	62
	RAPP	PR	82.4	8.0	100.0	0.0	3019	430
SPRING 2004	GW	CC	74.7	9.3	86.0	4.7	2189	190
	GW	SB	69.8	8.4	94.1	2.0	1359	130
	PIANK	BP	68.7	5.7	93.2	1.9	1495	140
	PIANK	PB	55.7	16.5	50.0	18.7	489	37
	RAPP	DG	38.0	14.4	88.5	11.2	770	48
	RAPP	PR	65.2	5.8	92.1	2.7	1462	152
SUMMER 2004	GW	CC	89.0	6.3	100.0	0.0	2601	197
	GW	SB	71.6	12.5	100.0	0.0	1424	141
	PIANK	BP	75.5	6.2	99.8	0.2	784	73
	PIANK	PB	87.5	5.1	100.0	0.0	1137	126
	RAPP	DG	30.4	15.4	50.7	21.9	389	19
	RAPP	PR	84.9	10.3	100.0	0.0	1395	119
FALL 2004	GW	CC	85.5	7.5	100.0	0.0	1599	115
	GW	SB	86.8	4.4	88.1	11.3	1455	101
	PIANK	BP	79.7	4.9	98.8	0.8	1456	129
	PIANK	PB	69.6	12.3	52.8	21.2	541	46
	RAPP	DG	36.3	17.4	68.0	19.8	506	19
	RAPP	PR	75.7	9.1	100.0	0.0	1293	112

[a]GW=Great Wicomico; PIANK=Piankatank; RAPP=Rappahannock
[b]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Appendix XVIII. Analysis of the effects of *Sample Date* and *Reef* on (A) % oyster shell reef particles and (B) % of reef particles with evidence of boring sponge (*Cliona* spp.) using Friedman's method by performing main-effects two-way ANOVA on data ranked within each date.

(A)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	1555	311	6.08	**<0.0001**
Reef	5	533	107	2.08	0.0698

(B)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	1555	311	4.59	**0.0006**
Reef	5	3541	708	10.45	**<0.0001**

Appendix XIX. Analysis of the effects of *Sample Date* on (A) % oyster shell reef particles and (B) % of reef particles with evidence of boring sponge (*Cliona* spp.) using Kruskal-Wallis tests by performing one-way ANOVA on ranked data for each reef.

(A)

Reef[a]	**Date DF**	**Type III SS**	**Mean Square**	**F-value**	**p**
CC	5	750	150	18.23	**<0.0001**
SB	5	427	85	2.53	0.0562
BP	5	878	176	4.76	**0.0037**
PB	5	796	159	3.95	**0.0094**
DG	5	380	76	1.32	0.2893
PR	5	759	152	5.07	**0.0026**

(B)

Reef[a]	**Date DF**	**Type III SS**	**Mean Square**	**F-value**	**p**
CC	5	556	111	1.72	0.1680
SB	5	339	68	0.86	0.5238
BP	5	572	115	1.65	0.1859
PB	5	605	121	1.78	0.1546
DG	5	462	92	1.24	0.3209
PR	5	536	107	1.51	0.2234

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Appendix XX. Analysis of the effects of *Sample Date* and *Reef* on one-sided surface area (mm^2) of individual reef particles (A) in a two-way ANOVA and (B) in an one-way ANOVA (see Results section for explanation).

(A)

Source	DF	Type III SS	Mean Square	F-value	p
Date	5	901178899	180235780	118.89	**<0.0001**
Reef	5	1633812190	326762438	215.55	**<0.0001**
Date x Reef	25	720812040	28832482	19.02	**<0.0001**

(B)

Source	DF	Type III SS	Mean Square	F-value	p
Reef	5	1929903954	385980791	224.74	**<0.0001**

Appendix XXI. Analysis of the effects of *Elevation* on the density of live and "box" oysters (# • m^{-2}) for (A) pooled data during 2003 and 2004 for crest and flank elevations only and (B) pooled data during 2004 only for all three elevations, using Kruskal-Wallis tests by performing one-way ANOVA on ranked data for each reef.

(A)

Live C.v.

Reef[a]	Elevation DF	Type III SS	F-value	p
CC	1	1067	0.72	0.4053
SB	1	7704	6.57	**0.0177**
BP	1	805	0.51	0.4825
PB	1	1625	0.88	0.3590
DG	1	2828	2.45	0.1319
PR	1	610	0.30	0.5905

"Box" C.v.

Reef[a]	Elevation DF	Type III SS	F-value	p
CC	1	2	0.00	0.9691
SB	1	2311	1.56	0.2248
BP	1	688	0.48	0.4936
PB	1	210	0.18	0.6725
DG	1	2471	2.82	0.1075
PR	1	852	0.90	0.3530

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Appendix XXI. (Continued)

(B)

Live C.v.

Reef[a]	Elevation DF	Type III SS	Mean Square	F-value	p
CC	2	275	138	0.17	0.8491
SB	2	5457	2728	4.95	**0.0224**
BP	2	595	297	0.54	0.5933
PB	2	2715	1358	1.64	0.2268
DG	2	8692	4346	10.33	**0.0015**
PR	2	2376	1188	1.21	0.3252

"Box" C.v.

Reef[a]	Elevation DF	Type III SS	Mean Square	F-value	p
CC	2	568	284	0.59	0.5685
SB	2	2901	1451	1.92	0.1811
BP	2	196	98	1.00	0.3911
PB	2	2667	1334	2.58	0.1092
DG	2	8433	4217	9.15	**0.0025**
PR	2	6357	3178	6.86	**0.0077**

[a]CC=Crane's Creek; SB=Shell Bar; BP=Burton's Point; PB=Palace Bar; DG=Drumming Ground; PR=Parrot's Rock

Appendix XXII. Two-way ANOVA of the effects of *Reef* and *Elevation* on live oyster shell height (mm). Data for 2004 only for all three elevations.

Source	DF	Type III SS	Mean Square	F-value	p
Reef	5	5004	1001	4.14	**0.0011**
Elevation	2	4237	2119	8.77	**0.0002**
Reef x Elev.	10	3916	392	1.62	0.0985

Appendix XXIII. Density of non-oyster epifauna (# • m^{-2}), ribbed mussel (G. demissa) abundance (# • m^{-2}) , % cover of non-oyster epifauna, % cover of barnacles (*Balanus* spp.) and white crust (*M. tenuis*). Data pooled for 2004 only for all three elevations. See Table 2 for taxa included in abundance and % cover groupings. Elevations are graphically described in Figure 3.

Elevation	# Non-Oyster Epifauna		# G. Demissa		% Non-Oyster Epifauna		% Belanaus spp.		% M. tenuis	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
CREST	84	38	80	38	45.1	4.2	18.3	2.3	35.0	3.5
FLANK	33	12	28	12	41.6	3.6	16.7	1.7	33.6	3.3
BASE	34	15	26	13	46.8	3.0	21.1	2.4	35.4	3.2

Appendix XXIV. Density of live oysters (# • m^{-2}) collected in quadrates along transects during summer and fall 2004 at Shell Bar reef.

Transect	Dist. From Crest (m)	% Dist. from Crest to Seabed	Oyster Abundance	Transect	Dist. From Crest (m)	% Dist. from Crest to Seabed	Oyster Abundance
1	0	0.0	48	1	0	0.0	48
	2	14.3	80		2	25.0	192
	4	28.6	176		4	50.0	176
	6	42.9	160		6	75.0	64
	8	57.1	96		8	100.0	0
	10	71.4	64	2	0	0.0	0
	12	85.7	112		2	33.3	0
	14	100.0	0		4	66.7	128
2	0	0.0	48		6	100.0	16
	2	25.0	240	3	0	0.0	48
	4	50.0	144		2	25.0	0
	6	75.0	144		4	50.0	96
	8	100.0	0		6	75.0	64
3	0	0.0	32		8	100.0	176
	2	20.0	80				
	4	40.0	32				
	6	60.0	96				
	8	80.0	128				
	10	100.0	0				

Appendix XXV. Density of live oysters (# • m^{-2}) collected in quadrates along transects during summer and fall 2004 at Palace Bar reef.

Summer 2004				Fall 2004			
Transect	Dist. From Crest (m)	% from Crest to Seabed	Oyster Abundance	Transect	Dist. From Crest (m)	% from Crest to Seabed	Oyster Abundance
1	0	0.0	0	1	0	0	0
	2	14.3	16		2	25	16
	4	28.6	0		4	50	0
	6	42.9	16		6	75	16
	8	57.1	144		8	100	16
	10	71.4	160	2	0	0	0
	12	85.7	48		2	20	0
	14	100.0	0		4	40	16
2	0	0.0	256		6	60	0
	2	16.7	32		8	80	0
	4	33.3	16		10	100	0
	6	50.0	96	3	0	0	112
	8	66.7	64		2	20	0
	10	83.3	240		4	40	0
	12	100.0	0		6	60	176
3	0	0.0	0		8	80	128
	2	11.1	32		10	100	96
	4	22.2	144				
	6	33.3	0				
	8	44.4	144				
	10	55.6	32				
	12	66.7	64				
	14	77.8	64				
	16	88.9	128				
	18	100.0	16				

Appendix XXVI. Data for the "painted shell" experiment, including the initial (T_0) # of shells deployed and the number remaining (T_1) when retrieved.

River	Reef	Elevation	# Shells T_0	# Shells T_1	# Flipped	# Nearby
GW	CC	CREST	16	5	2	3
		FLANK	16	9	7	0
	SB	CREST	16	14	7	0
		FLANK	16	16	5	0
PIANK	BP	CREST	16	9	8	4
		FLANK	16	13	6	0
	PB	CREST	16	16	10	0
		FLANK	16	16	4	0
RAPP	DG	CREST	16	15	2	0
		FLANK	16	12	5	0
	PR	CREST	16	5	5	0
		FLANK	16	16	6	0