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TOWARD DESIGN CRITERIA IN CONSTRUCTED OYSTER REEFS: OYSTER RECRUITMENT AS A FUNCTION OF SUBSTRATE TYPE AND TIDAL HEIGHT

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ABSTRACT Restoration of degraded oyster reef habitat generally begins with the addition of substrate that serves as a reef base and site for oyster spat attachment. Remarkably, little is known about how substrate type and reef morphology affect the development of oyster populations on restored reefs. Three-dimensional, intertidal reefs were constructed near Fisherman's Island, Virginia: two reefs in 1995 using surfclam (*Spisula solidissima*) shell and six reefs in 1996 using surfclam shell, oyster shell, and stabilized coal ash. We have monitored oyster recruitment and growth quarterly at three tidal heights (intertidal, mean low water, and subtidal) on each reef type since their construction. Oyster recruitment in 1995 exceeded that observed in the two subsequent years. High initial densities on the 1995 reefs decreased and stabilized at a mean of 418 oyster/m^2. Oyster settlement occurred on all reef types and tidal heights in 1996; however, postsettlement mortality on the surfclam shell and coal ash reefs exceeded that on the oyster shell reefs, which remained relatively constant throughout the year (mean = 935 oysters/m^2). Field observations suggest that predation accounts for most of the observed mortality and that the clam shell and coal ash reefs, which have little interstitial space, suffer greater predation. Oyster abundance was consistently greatest higher in the intertidal zone on all reefs in each year studied. The patterns observed here lead to the preliminary conclusion that the provision of spatial refugia (both intertidal and interstitial) from predation is an essential feature of successful oyster reef restoration in this region. In addition, high levels of recruitment can provide a numerical refuge, whereby the oysters themselves will provide structure and increase the probability of an oyster population establishing successfully on the reef.

KEY WORDS: oyster, *Crassostrea virginica*, habitat restoration, recruitment substrate, intertidal, Virginia

INTRODUCTION

The marked decline in oyster resources in the mid-Atlantic region throughout much of this century have been attributed primarily to increased harvest pressure, a direct consequence of ineffective resource management (Haven et al. 1978, Rothschild et al. 1994, Frankenberg 1995). Furthermore, the increased prevalence of the protistan parasites *Perkinsus marinus* ("Dermo") and *Haplosporidium nelsoni* ("MSX") (Burreson and Ragone 1996) and over-all environmental degradation have accelerated declines in oyster numbers over the last three decades. There is a general consensus that oyster reefs were once a dominant feature of much of the lower Chesapeake Bay, contributing considerable biological and geological structure to the system. Historically, oysters in this system likely affected systemwide trophic structure and water quality (Newell 1988, Ulanowiz and Tuttle 1992), while providing considerable physical structure, which, in turn, facilitated the development of diverse benthic communities. The need to restore oyster resources and oyster reefs, not only for their direct harvest but also for the ecological services they provide, has been recognized recently (Lenihan 1996, Coen and Luckenbach in press, Coen et al. 1999).

To date, efforts to restore the resource have been focused in areas where the oysters were abundant and extensive but have been reduced to subtidal "footprints" of former reefs. Restoration attempts carried out in areas previously devoid of oysters (as described herein) have been few. Typically, restoration of a degraded oyster reef has involved the addition of substrate to serve as a reef base and site for spat attachment and subsequent oyster growth. Oyster shell resources and/or the funds to purchase them are often in limited supply; therefore, the interest in evaluating both how to use oyster shell most effectively and the efficacy of using alternative substrates as reef bases is considerable. Attention has recently been given to the importance of vertical relief of reefs on oyster growth, survival, and disease dynamics (Bartol and Mann in press; Lenihan et al. 1996, Lenihan and Peterson 1998); however, there remains a paucity of information on the degree of relief necessary to maximize oyster settlement, recruitment, and subsequent survival. Furthermore, numerous studies have investigated the use of alternative substrates to oyster shell (Soniat et al. 1991, Haywood and Soniat 1992, Haywood et al. in press). These studies have generally been laboratory or small-scale field experiments and have not clarified how these substrates might be used to maximize oyster recruitment, growth, and survival in the context of large-scale reef restoration. These issues have increasing relevance as restoration efforts proceed throughout the extensive range of the eastern oyster. This report focuses on a large-scale field experiment in the lower Chesapeake Bay, Virginia, which related oyster recruitment, growth, and survival to reef substrate types and tidal height. The results have relevance for the choice and placement of materials and the development of design criteria for oyster reef restoration.

SITE DESCRIPTION

The study site is located near Fisherman's Island, Virginia, U.S.A., in the vicinity of the mouth of Chesapeake Bay (Fig. 1). This is a polyhaline site with a tidal amplitude of approximately 1.25 m. Marsh islands, intertidal flats, and subtidal bottom within the area are all owned by the Commonwealth of Virginia and the

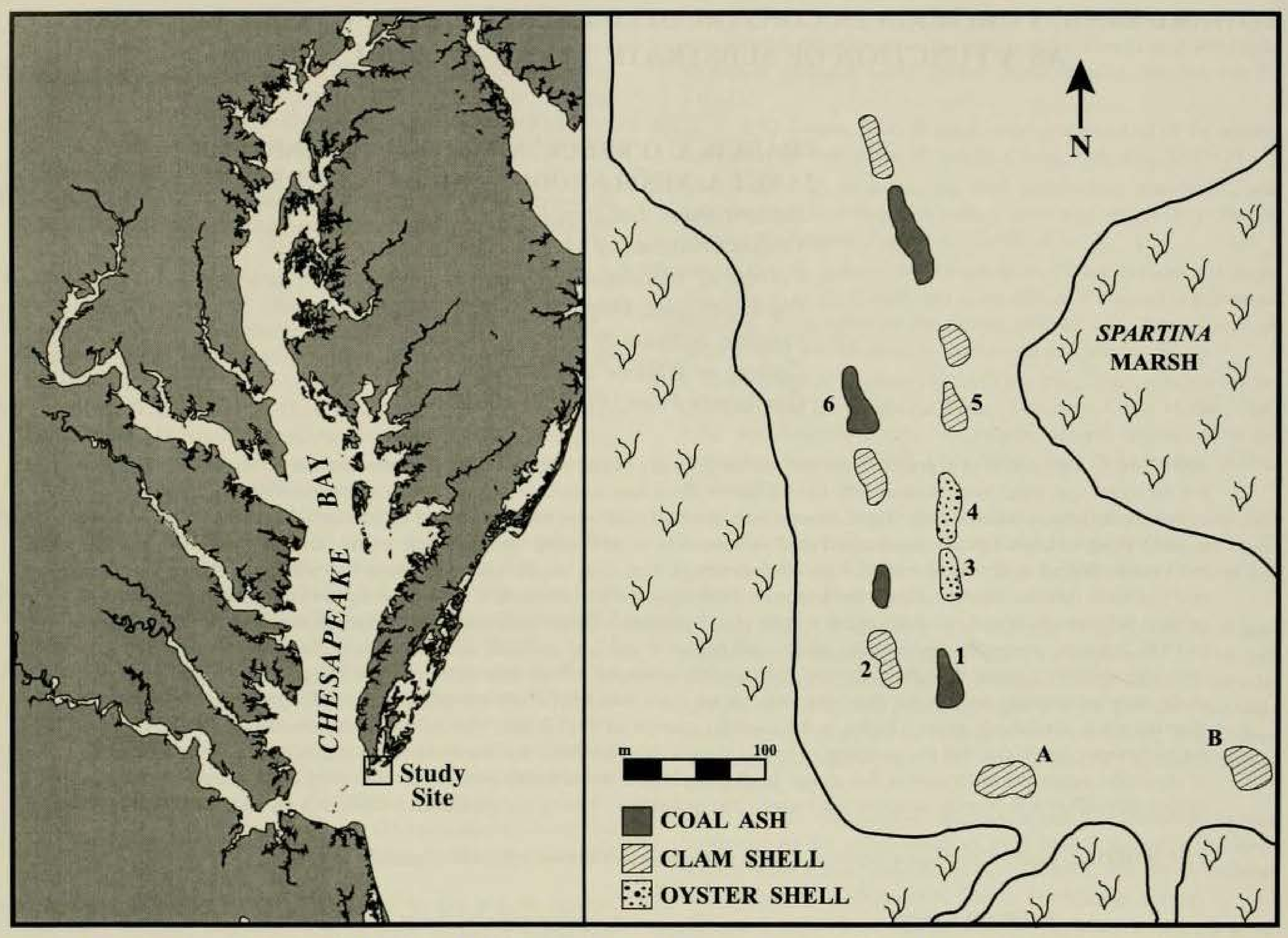

Figure 1. Location of study area near Fisherman's Island, Virginia. Reefs with an alphanumeric label were monitored continually throughout the period of the study. Reefs are not drawn to scale.

federal government and are managed by the U.S. Fish and Wildlife Service as part of the Eastern Shore of Virginia National Wildlife Refuge. In April 1995, two intertidal reefs, approximately 8,000 m^2 (2 acres) each, were constructed at the site as part of a remediation project funded by the Chesapeake Bay Bridge Tunnel District. The reefs were created by placing approximately 40,000 Virginia bushels (~ 1,973 m^3) of surfclam (*Spisula solidissima*) shells on two intertidal mudflats (see A and B in Fig. 1). The reefs extended from ~ 0.5 m below to 0.5 m above MLW. The reef designated A in Figure 1 had greater surface area at higher tidal elevation than reef B. Irregular patterns of mounds, ridges, and furrows existed across the reef surface as a result of the planting technique (deployment from barges by water cannon). Hereafter, the clam shell reefs, constructed in 1995, are designated as 95 Clam reefs.

Eleven additional reefs (Fig. 1) were constructed in 1996 with funding from the Aquatic Reef Habitat Program, Virginia Power Company, and the Virginia Oyster Repletion program. Five of these reefs were constructed with surfclam shells, two with oyster (*Crassostrea virginica*) shells, and four with stabilized coal combustion by-products (fly ash). The latter material, constructed using 88% fly ash stabilized with 12% (w:w) Portland cement, is described in greater detail in Andrews et al. (1997) and has been shown to provide an environmentally suitable substrate for oyster settlement and growth (Alden et al. 1996). Limited availability of oyster shells resulted in the smaller number of reefs ($n = 2$) constructed with that material. A total of 39,920 bushels (1,965 m^3) of surfclam shells, 7,000 bushels (325 m^3) of oyster shell, and 20,150 bushels (994 m^3) of coal-ash pellets were used to construct the reefs. Two reefs of each substrate type, ranging in size from 162 to 364 m^2, were selected for monitoring (reefs 1–6 in Fig. 1). The reefs were oriented in a north–south direction, with seven reefs in one row and four reefs in another row to the west. A channel ranging in width from 10 to 40 m separates the two rows. Hereafter, the reefs constructed in 1996 are designated as Oyster, 96 Clam, and Ash.

MATERIALS AND METHODS

Quadrate Sampling

Sampling of the reefs for determination of oyster abundance and size was initiated in October 1995. On each of the reefs selected for monitoring (two of each substrate type; A, B, and 1–6 in Fig. 1), quadrate samples ($n = 3$) were collected from each of three tidal heights. The tidal heights were 0.25 m below mean low water (hereafter called Subtidal), at mean low water (hereafter called MLW), and 0.25 m above MLW (hereafter called Intertidal). Replicate quadrates (0.0625 m^2; $n = 3$) were placed haphazardly within each tidal height stratum (Subtidal, MLW, and Intertidal) on replicate reefs ($n = 2$) of each reef substrate type

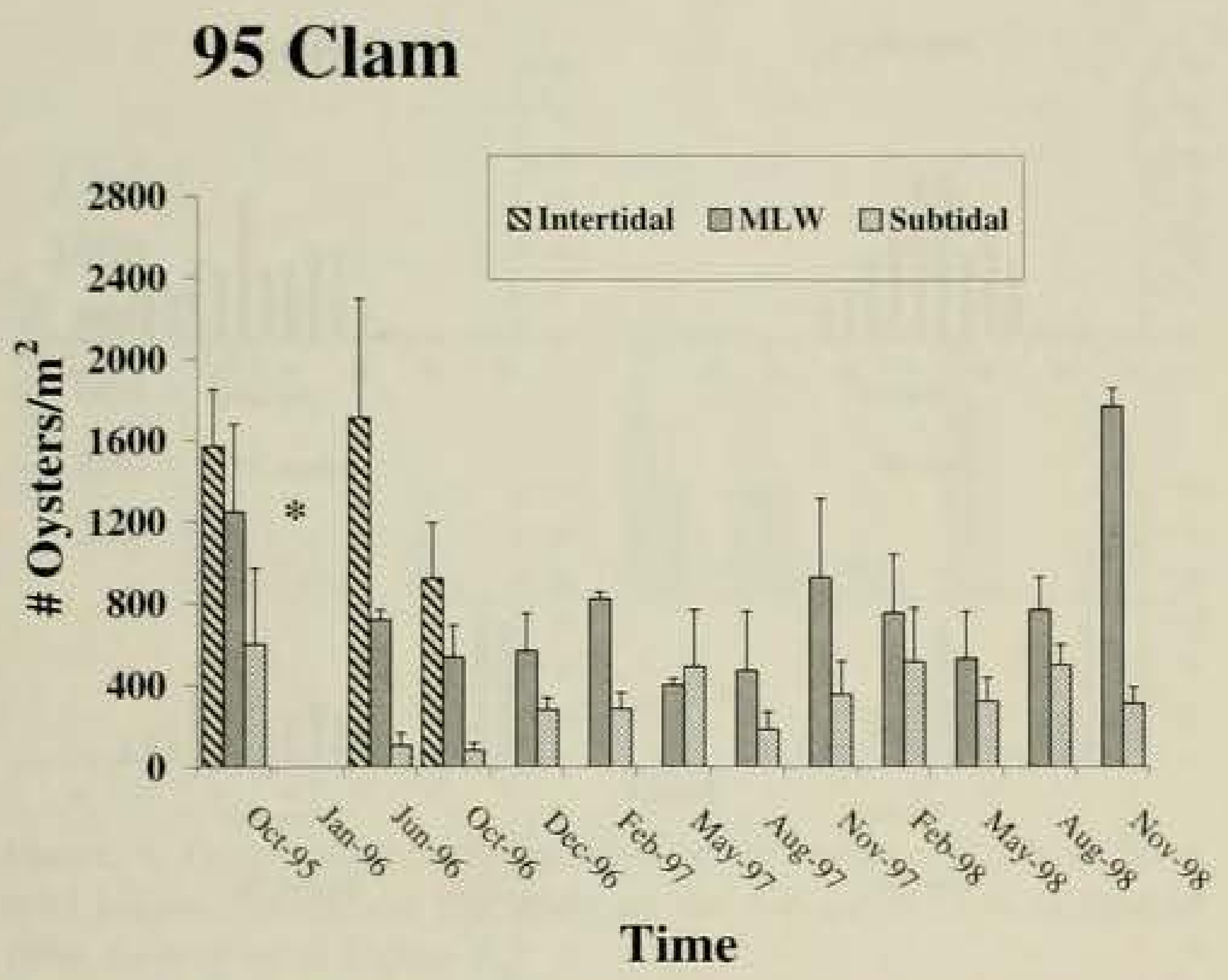

Figure. 2. Oyster abundance (number per m², mean ± SD) from three tidal heights throughout the study on the 95 Clam shell reefs. * No replicate quadrates were taken during this sampling period.

(Oyster, 95 Clam, 96 Clam, and Ash) to give a maximum of 72 samples per sampling period. Within each quadrate sample, all reef substrate was retained to a depth of 15 cm but did not include underlying sediments if encountered. Samples were transported to the laboratory on ice (if necessary) and were processed immediately. Processing involved the enumeration of all live oysters in each sample. In addition, 50 oysters from each tidal height, on each reef sampled, were measured to the nearest 0.1 mm. Sampling took place on a quarterly basis in an attempt to detect seasonal changes in oyster abundance.

Interstitial Space Estimates

The volume of interstitial space for each of the substrates used to construct reefs in 1996 was estimated using subsamples of the substrates before the deployment of the substrates. All of the subsamples used were considered the ideal for that substrate type: whole (with some partially fragmented) oyster and surfclam shells and ash pellets ≈ 5 cm in diameter. Interstitial volume was calculated using the volumetric displacement of the substrate packed to the top of a container (≈5.85 L). This displacement value was then subtracted from the container volume to give interstitial volume. All interstitial volumes were corrected to reflect the substrate type within a 1-L container. This process was carried out five times for each substrate in order to generate mean and standard deviation values. These values were then compared using a one-way analysis of variance ANOVA.

Statistical Analysis

The 95 clam reefs were not compared statistically with the 1996 reefs because of the dual confounding effects of temporal difference in deployment and considerable differences in surface areas of the reefs. Summary statistics generated for oyster densities and sizes by reef type are reported in graphical form.

Over the course of the study, some tidal height strata on some of the 1996 reefs were much reduced as a result of settling and/or erosion, thus we were unable to complete sampling from all tidal heights for the duration of the study. Therefore, for the purpose of comparing the abundance of oysters by substrate, we confined our analysis to the subtidal samples, for which there is a complete set of samples. Abundances were log transformed [ln (x+1)] to conform to normality assumptions as required. A two-way ANOVA was carried out (with substrate type and time as the main effects) to ensure that there was no interaction term. Upon satisfaction of this criterion, a randomized complete block design ANOVA was conducted using substrate type as the main effect blocked by time (Sokal and Rohlf 1981, pp. 345–352). The 96 Clam reefs had returns from all tidal heights for all time periods bar one (one reef in November 1997). Therefore, we were able to compare oyster abundances from all tidal heights of the 96 Clam reefs. The values from these tidal heights were compared accordingly. The Oyster reefs had complete returns from the MLW and subtidal samples for the two replicate reefs, resulting in valid comparisons of these tidal heights blocked according to time.

RESULTS

At the initial sampling of the 95 Clam shell reefs in October 1995, high oyster numbers were recorded at all tidal heights (Fig. 2). The intertidal samples had the highest oyster numbers throughout, followed by the MLW and subtidal samples, respectively. Subsequently, oyster abundances declined precipitously at all tidal heights. By November 1996, the elevations of the reefs were reduced through subsidence, compaction, and/or erosion to the point that intertidal samples could not be retrieved (Fig.2). Despite some fluctuations, the numbers of oysters on these reefs tended to remain stable in the following sampling periods. Throughout this period, the abundance of oysters remained fairly constant, mean values for the MLW and subtidal samples were 834 oysters/m² and 345 oysters/m², respectively. There were no appreciable differences in size distribution among the tidal heights through the sampling periods. Therefore, the size frequencies from each tidal height within each sampling period were pooled, and these are graphically represented in Figure 3. A unimodal population distribution is apparent for the first year of the monitoring (October 1995 to September 1996). Following a small recruitment event in December 1996 (Fig. 3), a bimodal population distribution was evident. Between August 1997 and November 1997, mortality among larger animals and an influx of small, newly recruited individuals was apparent. Thereafter, the size distribution on these reefs remained relatively stable, with small, newly recruited individuals dominating in terms of over-all abundance (Fig. 3).

Relatively low numbers of oysters were present in the Ash reef samples from December 1996 through August 1997 (Fig. 4). In November 1997, the young-of-the-year animals were detected on the reef and increased the over-all number of oysters sampled. The recruitment event in each year sampled was followed by a rapid decline in the numbers of oysters found on the reefs. Also, throughout the sampling of the Ash reefs, the intertidal stratum consistently contained higher oyster densities than the other tidal heights. The MLW stratum for the most part, had greater oyster densities than the subtidal stratum. The size distribution of oysters on the ash reefs was highly variable, with smaller oysters (< 25 mm) dominating throughout and larger oysters rare (Fig. 5).

The 96 clam reefs displayed patterns similar to the Ash reefs in terms of over-all recruitment patterns and abundances (Fig. 6). Again, relatively low densities were found each sampling period. Recruitment events were followed by a sharp decline in oyster densities. Intertidal stratum had greater oyster densities than the other two tidal heights in all but two sampling periods (November

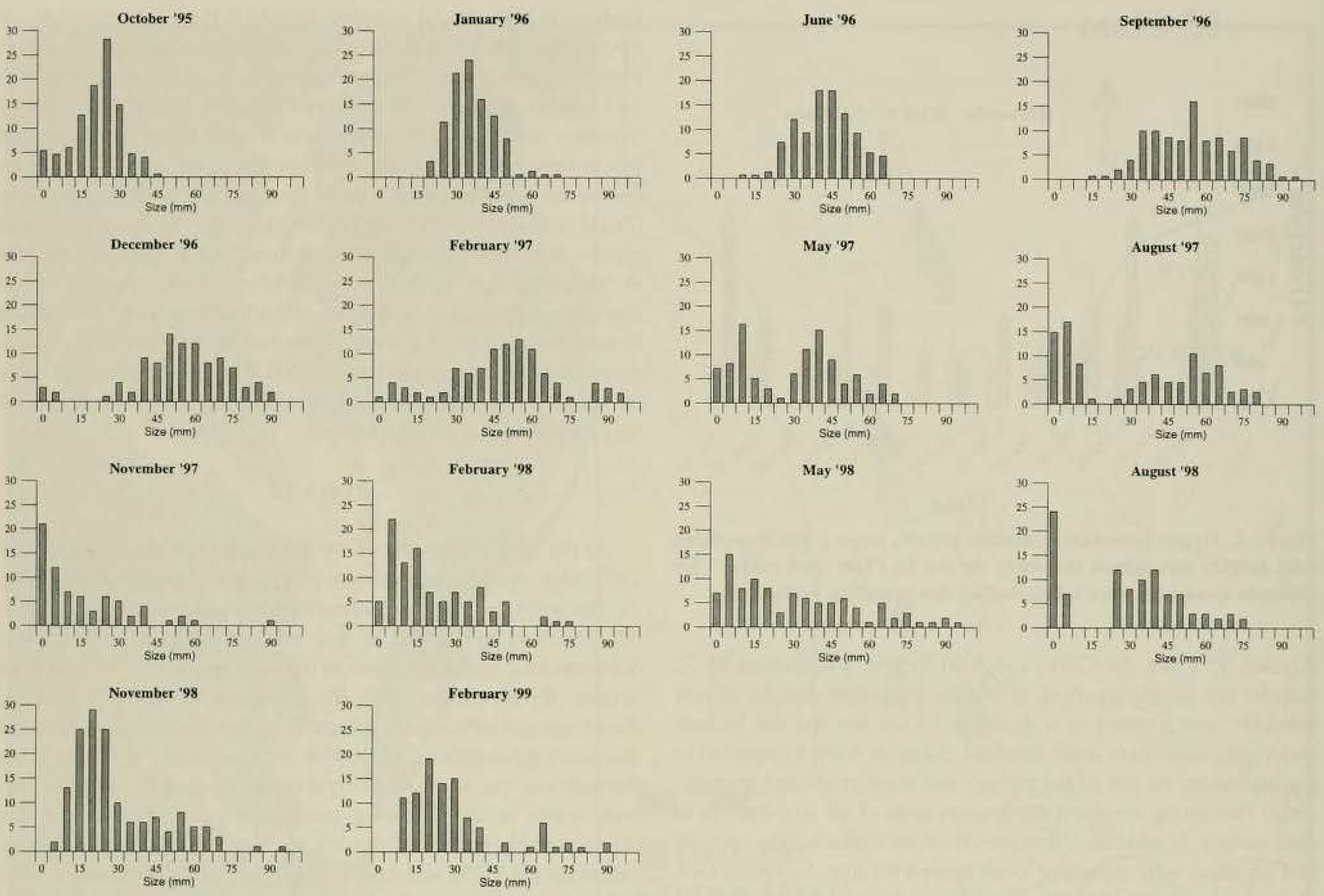

Figure. 3. Oyster size frequency distribution over the course of the study from the 95 Clam shell reefs. Size distributions were all animals combined from the three tidal heights.

1997 and August 1998). The size distributions within each sampling period was indicative of a population dominated by small oysters (< 20 mm; Fig. 7). However, in later sampling periods, there was a greater proportion (albeit small) of larger oysters on the 96 Clam reefs than found on the Ash reefs.

In 1996, in contrast to the low recruitment of oysters found on the reefs of coal ash and clam substrate, the Oyster reefs had a modest recruitment in December 1996 (Fig. 8). Survival on the oyster reef was greater than on the other substrate types, and again oyster densities were greater intertidally than at the other two tidal heights. The size distribution of oysters on the oyster shell reefs was approaching a unimodal normal distribution by May 1997 (Fig. 9). Recruitment events detected in November of subsequent years resulted in a bimodal size distribution. However, relatively large numbers of larger oysters persisted on the reefs.

Interstitial volumes differed significantly among the substrate types (Table 1). The oyster shell interstitial volume (0.7 L interstitial volume/1 L of substrate) was significantly greater than the volumes of both the clam (0.58 L) and coal ash (0.45 L) substrates. Analysis of variance of oyster densities from Subtidal samples detected significant differences among the Oyster, Ash, and Clam substrates (Table 2a). The Oyster substrate had significantly greater numbers of live oysters than the other reef types (Table 2a). The Intertidal samples from the 96 Clam reefs had significantly greater densities of oysters than the Subtidal samples (Table 2b). In addition, the densities of oysters found in the MLW samples were significantly greater than those found in the Subtidal samples on the Oyster shell reefs (Table 2c).

DISCUSSION

The reef bases at Fisherman's Island, Virginia, have all persisted, but quite different oyster populations have developed depending upon both the year of deployment and the substrate type used. Reduced elevations were observed in all reef bases, likely the result of some combination of subsidence, compaction, and erosion. Although interstitial volume estimates differed among the substrate types used on the 1996 reefs (Table 1), subsequent (mis) handling of the clam shells and large-scale production of the ash substrates (hence, poor quality control) resulted in additional compaction. These factors served to further the disparity between the oyster shell and the other substrates in terms of interstitial volume. This variation, we believe, had very significant consequences for the development of resident oyster populations as discussed below.

Oyster recruitment levels varied across the region over the duration of the study. As part of the ongoing yearly monitoring of oyster reproduction in the lower Chesapeake Bay, the Virginia Institute of Marine Science (VIMS) uses spatfall collectors (shellstrings) to determine patterns and levels of oyster recruitment (unpublished data, Virginia Oyster Spat Survey, 1970 to 1998, VIMS). During 1996 and 1997, recruitment estimated from the shellstrings at Fisherman's Island was lower in magnitude and later in each year compared with the 1995 shellstring results. This pattern was consistent with observations throughout the lower bay (Morales-Alamo and Mann 1996, Morales-Alamo and Mann 1997). Sampling on the reef surfaces was not timed specifically to record early postsettlement abundance. Other studies have shown

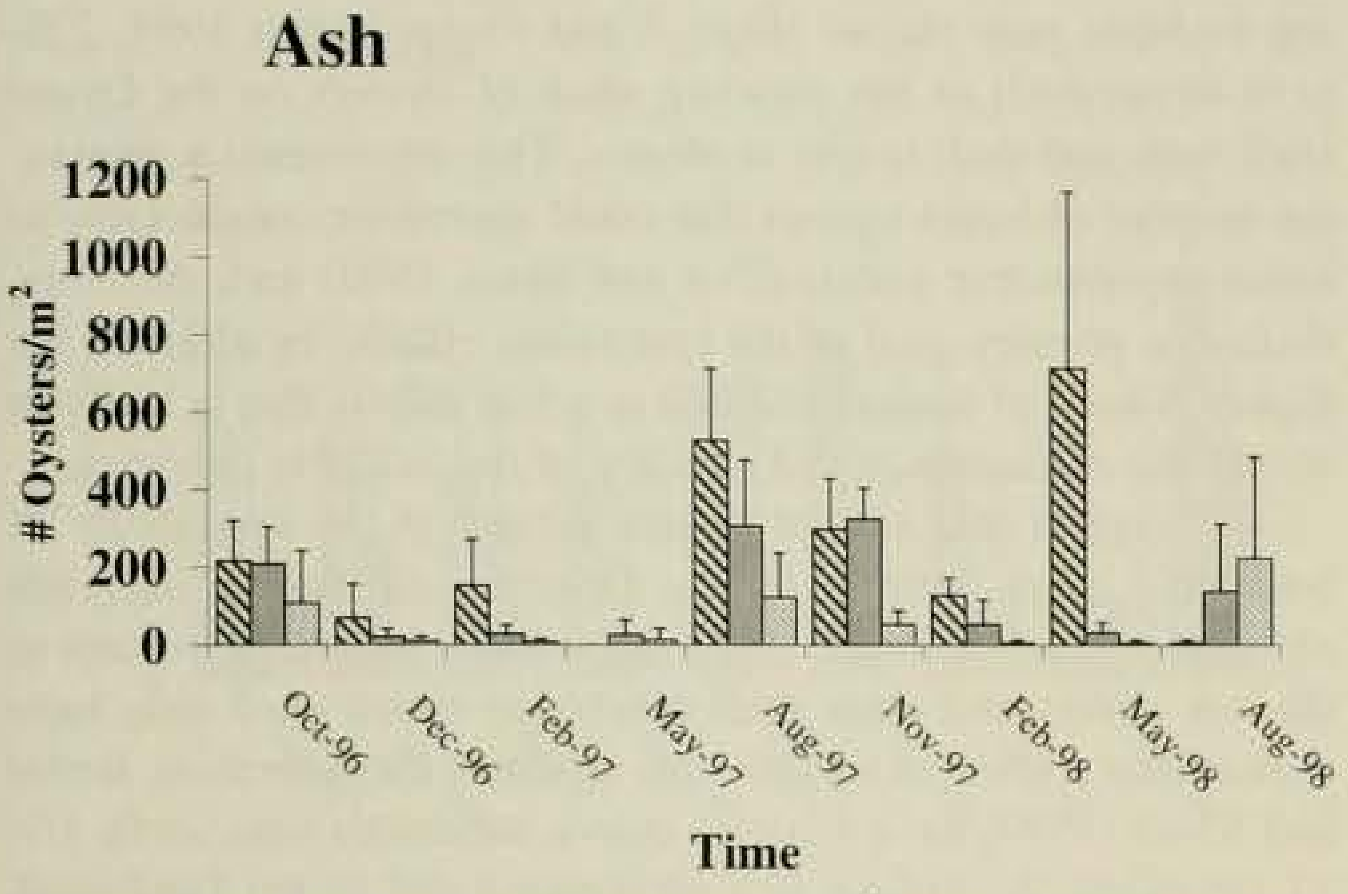

Figure. 4. Oyster abundance (number per m^2, mean ± SD) from three tidal heights throughout the study on the Ash pellet reefs planted in 1996. Legend as in Figure 2.

coal ash pellets (Alden et al. 1996, Andrews et al. 1997) and surfclam shells (Luckenbach unpublished data) are suitable substrates for oyster settlement. We would expect that early postsettlement densities, scaled to available substrate area, were comparable across reef type, but we lack confirming data.

Postsettlement survival of oysters varied in relation to tidal elevation, but the patterns were partially confounded by the loss of some tidal elevations from some reefs. The general trend observed was one of greater survival of oysters in the intertidal (Figs. 2, 4, 6, and 8), which is consistent with other studies conducted in the mid and southern Atlantic states of the U.S. (Kenny et al. 1990, Michener and Kenny 1991, O'Beirn et al. 1995, O'Beirn et al. 1996, Roegner and Mann 1995). Despite some variations in this pattern, significant differences were apparent for 96 Clam reefs, for which we have all tidal elevations present (Table 2b). In addition, oyster densities varied on the Oyster reefs between the two tidal heights evaluated (Table 2c). However, in the case of the Ash reefs, this trend was reversed on the final sampling period, with oysters virtually absent from intertidal samples (Fig. 4). These findings serve to highlight the importance of vertical relief when constructing oyster reefs in such environments as Fisherman's Island.

Variation in oyster abundance across substrate type was evident at all tidal heights (compare Figs. 4, 6, and 8), but because of missing levels on some reefs, statistical comparisons by substrate type were made only for the subtidal level (Table 2a). The significant trend of greater abundance of oysters on the Oyster reefs compared to the Ash reefs and 96 Clam reefs at this tidal level was evident throughout. Over-all mean density on the Oyster shell reef (935/m^2) exceeded that on the 96 Clam shell reef (149/m^2) and the Ash reef (141/m^2) roughly sixfold. Visual comparisons of the reefs are even striking. The Oyster shell reefs supported an uninterrupted layer of live oysters, which was not apparent on the other substrates, both of which had only sporadic clusters of oysters. In addition, the clam shell and coal-ash pellets reefs mostly retained

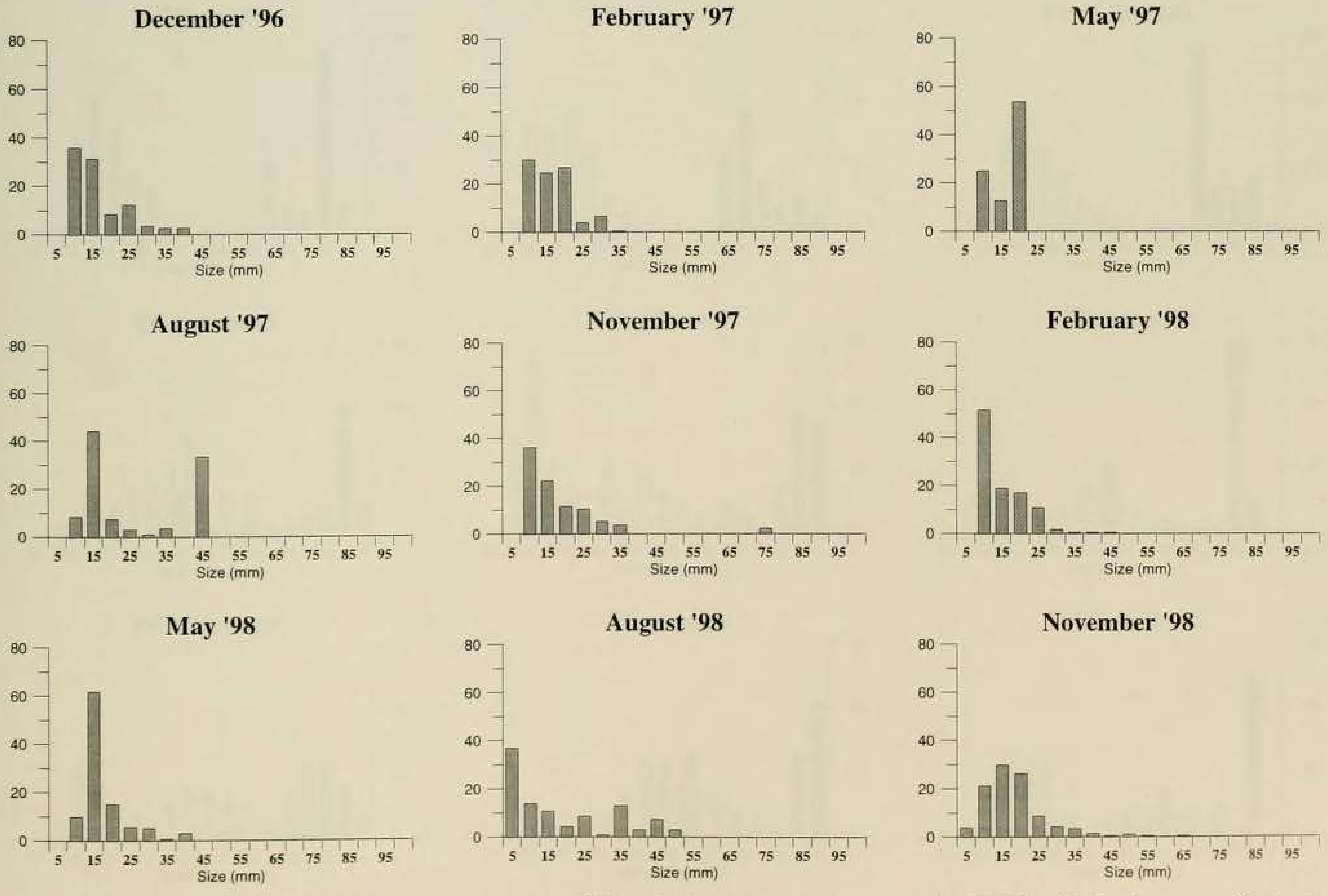

Figure. 5. Oyster size frequency distribution over the course of the study from the Ash reefs planted in 1995. Size distributions were all animals combined from the three tidal heights.

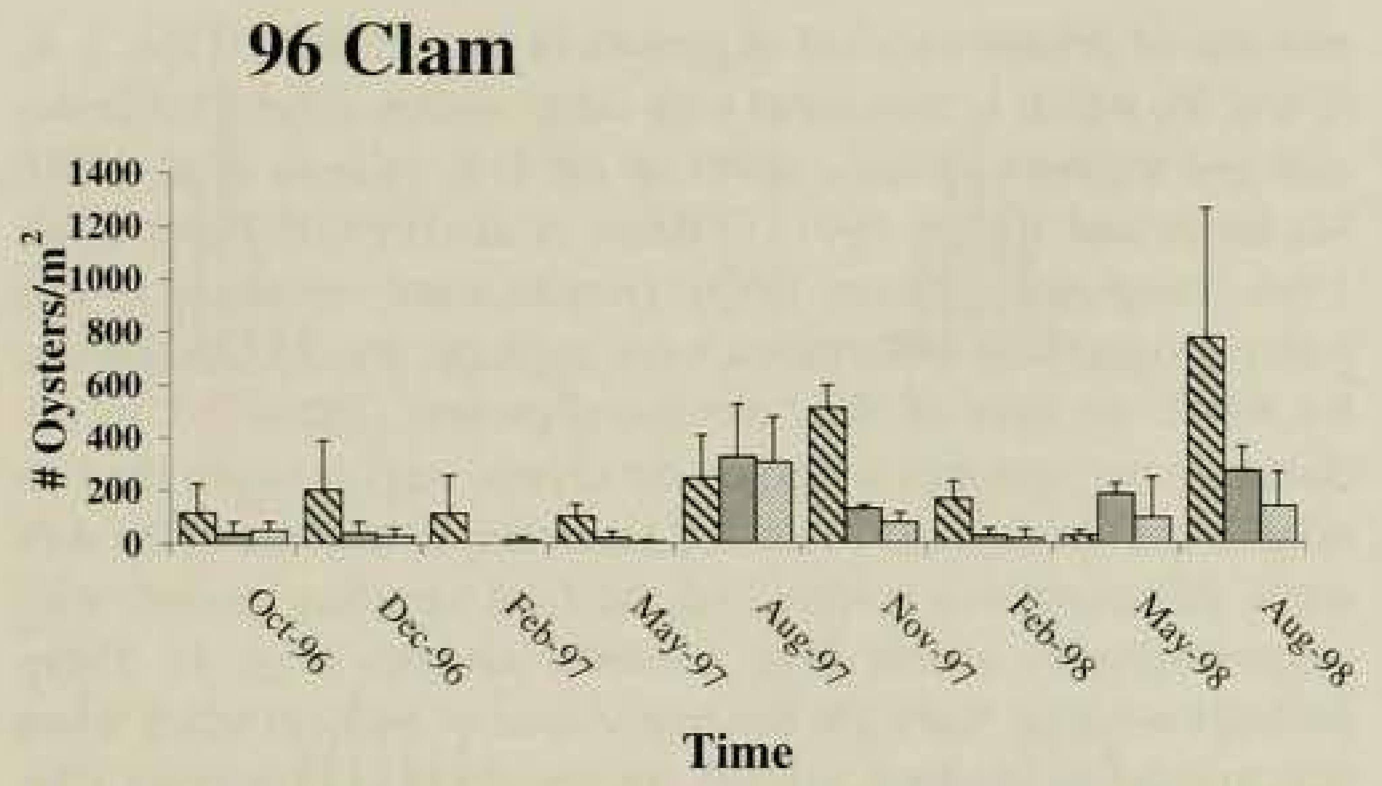

Figure. 6. Oyster abundance (number per m², mean ± SD) from three tidal heights throughout the study on the 96 Clam shell reefs. Legend as in Figure 2.

their original bleached white and dark gray colors, respectively, throughout the study, which is indicative of little or no biotic development on the reefs.

The dominance of the oyster shell substrate was further underscored when examining the size data of oysters from each of the substrate types. Small oysters (< 20 mm) dominated both the Ash and 96 Clam substrates (Figs. 5 and 7) throughout the entire monitoring period. There was no persistence of larger (older) oysters in either of these reef types. The 95 Clam reefs and the Oyster shell reefs had relatively greater proportions of larger oysters representing multiple year classes (Figs. 3 and 9). In August 1998, 22% (138 oysters/m²) of the standing stock of oysters on the Oyster shell reefs had shell height ≥ 60 mm. This represented a substantial number of larger oysters that could contribute considerably to future reproductive events (Cox and Mann 1992) and, therefore, realizes a primary goal of the restoration efforts. In addition, the higher density of oysters resulted in a reef matrix that is likely to ensure the maintenance and stability of the valuable interstices.

We suggest that several factors related to the availability of interstitial space account for the observed differences in oyster abundance across the reefs. First, the reduced interstitial volume in the ash pellets and clam shell relative to oyster shell may have reduced the amount of surface area available for settlement. Bartol and Mann (1999) have reported oyster settlement onto shells 10–15 cm below the surface in a constructed reef in the Piankatank River, Virginia, and J. Nestlerode and F. O'Beirn (unpublished data) have made similar observations in substrate baskets buried in these reefs at Fisherman's Island. The density estimates we report here include oysters collected to a depth of 15 cm scaled to a flat surface area of the reef and do not account for subsurface area that might be available for oyster attachment. Thus, oyster settlement onto the Oyster shell reefs may have exceeded those on the Ash and 1996 Clam shell reefs. Because recruitment levels were low, however, and attachment surface was not in limited supply, it is unlikely that settlement differences accounted for most of the variation across reef type.

Differential mortality of oysters at the surface and below the

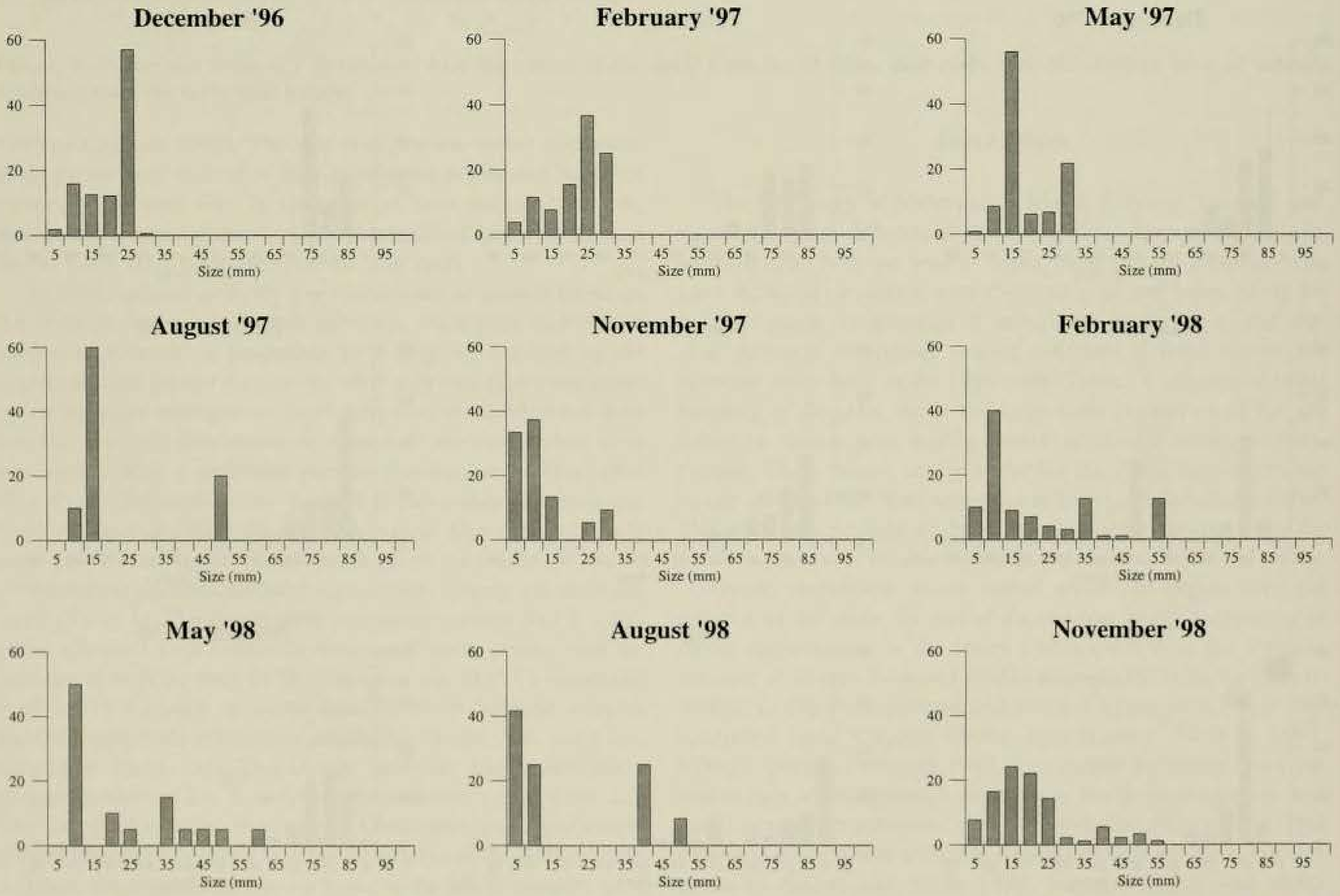

Figure. 7. Oyster size frequency distribution over the course of the study from the 96 Clam shell reefs. Size distributions were all animals combined from the three tidal heights.

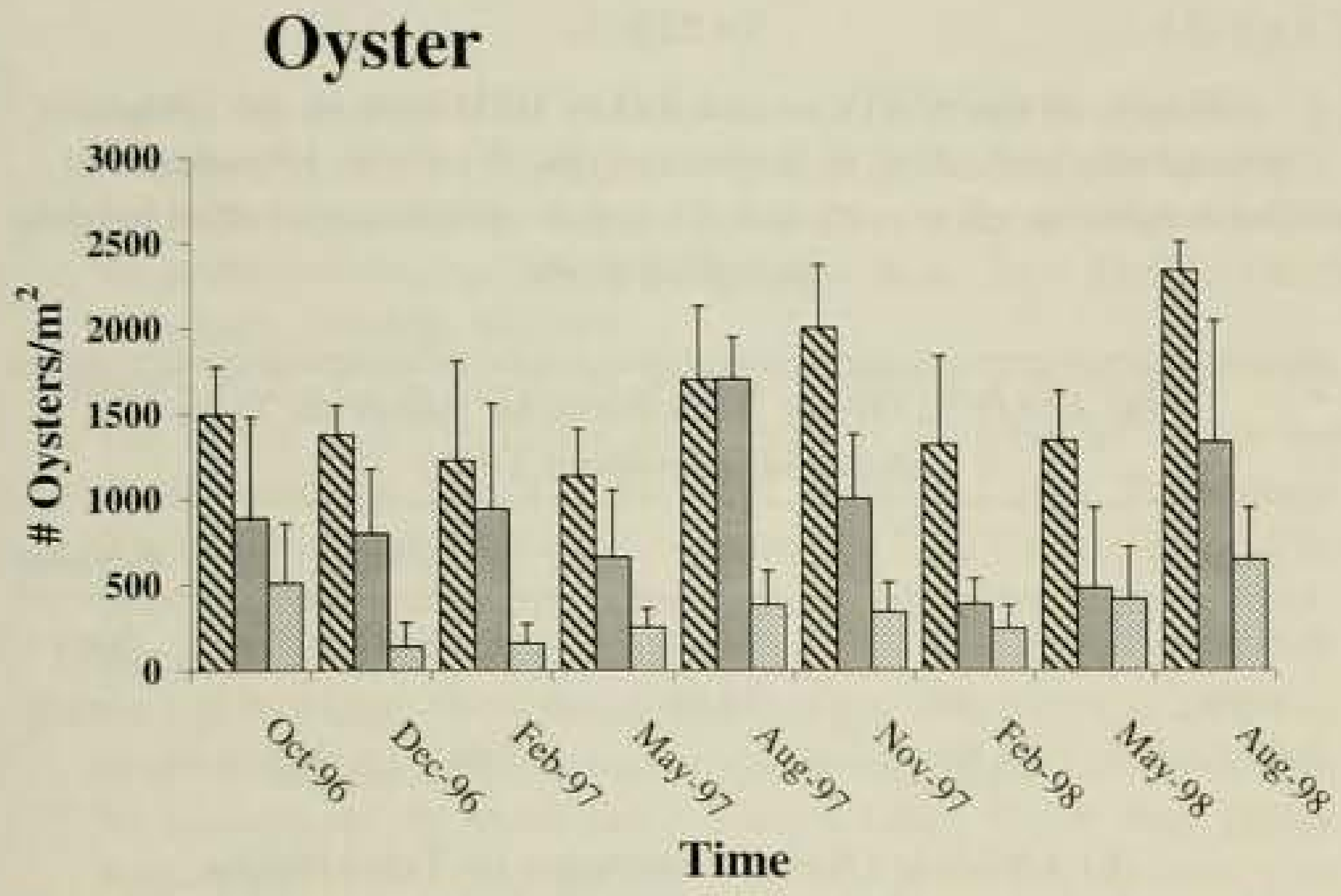

Figure. 8. Oyster abundance (number per m², mean ± SD) from three tidal heights throughout the study on the Oyster shell reefs planted in 1996. Legend as in Figure 2.

surface of the reefs is a likely explanation for the abundance patterns we observed. Bartol and Mann (1999) have demonstrated the value of interstitial space in aiding the survival of young oysters. The refuge afforded by the interstices protects the young oysters from predation and buffers them from climatic extremes. The considerably lower levels of interstitial space located on the clam shell and ash reefs most likely resulted in increased exposure of the young oysters to potential predators and other detrimental environmental factors (see reviews by Shumway 1996, White and Wilson 1996).

Finally, we expect a degree of positive density dependence in the development of oyster populations on constructed reefs. If the initial settlement and survival of oysters is sufficient (in part because of factors above), living oysters come to dominate the surface features of the reef and contribute to further interstitial space. In effect, the oysters themselves provide a refuge in numbers. In addition, the presence of large numbers of resident oysters in subsequent years may enhance settlement through the release of water-soluble settlement-inducing peptides (Tamburri et al. 1992, Turner et al. 1994). For example, the large recruitment event in 1995 (Fig. 2) was sufficient to result in a veneer of living oysters covering most of the clam shell substrate. Thus, when a smaller recruitment event occurred in 1996, the 95 Clam reefs and the 96 Clam reefs presented quite different habitats for new recruits and both recruitment and survival were greater on the older clam shell reefs (compare Figs. 2 & 3 with Figs. 6 & 7). Similarly, the abundances of oysters and spatial complexity of the oyster shell reefs have been increasing since their planting in 1996. Both the 96 Oyster shell reefs and the 95 Clam shell reefs developed abundant oyster densities, with multiple year classes present and reef surfaces dominated by living oysters. In contrast, the Ash reefs and the 96 Clam reefs have failed to develop abundant oyster populations, and generally only supported small size classes, which diminished in abundance after recruitment events.

Our findings suggest that in areas and years with high oyster

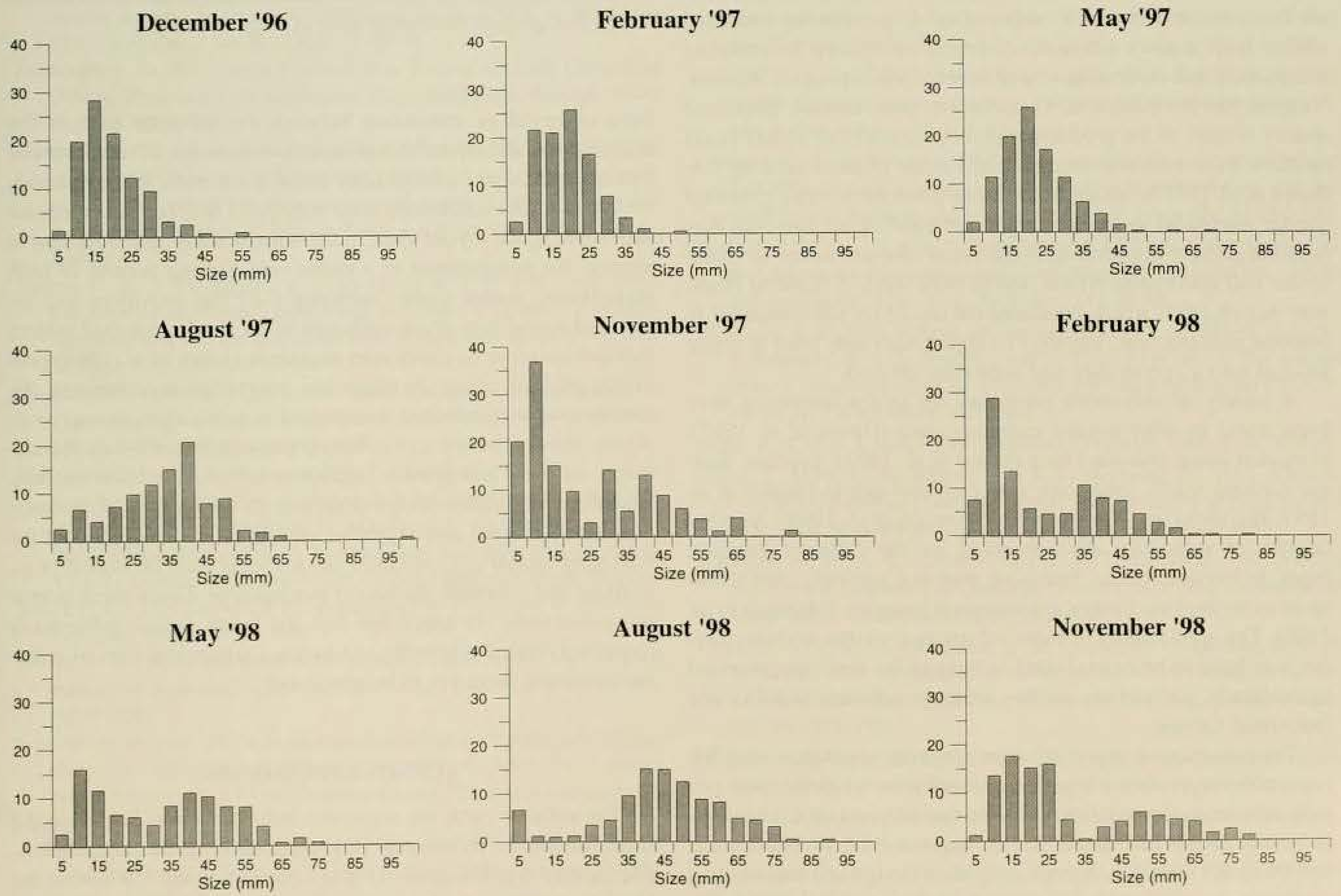

Figure. 9. Oyster size frequency distribution over the course of the study from the Oyster shell reefs planted in 1996. Size distributions were all animals combined from the three tidal heights.

TABLE 1.

ANOVA and Tukey HSD tests on interstitial space obtained from the three substrate types.

ANOVA: Interstitial Volume by Substrate Type

Source	df	SS	F Value	*P*-value
Substrate	2	0.156	42.8	0.0001
Error	12	0.178		
Tukey test		Oyster	Clam	Ash
Mean volumes (SD)		0.7 L (0.04)	0.58 L (0.06)	0.45 L (0.02)

Interstitial volume given as interstitial volume in liters per 1-L substrate.

TABLE 2.

Results of the ANOVAs and Tukey HSD tests on (a) oyster abundance according to substrate type, (b) oyster abundance at tidal heights on clam reef, and (c) oyster abundance at tidal heights on oyster reefs.

(a) ANOVA: Oyster Abundance by Substrate Type (Subtidal Elevations Only)

Source	df	SS	F Value	*P*-Value
Substrate	2	74.39	28.09	.0001
error	43	56.94		
Tukey test:	Oyster		Clam	Ash

(b) ANOVA: Oyster Abundance by Tidal Height (Clam Shell Reefs Only)

Source	df	SS	F Value	*P*-Value
Tidal height	2	14.85	4.01	.0263
error	38	70.35		
Tukey test:	Intertidal		Mean Low Water	Subtidal

(c) ANOVA: Oyster Abundance by Tidal Height (Oyster Reefs Only)

Source	df	SS	F Value	*P*-Value
Tidal height	1	8.99	29.86	.0001
error	26	7.83		
Tukey test	Intertidal		Mean Low Water	

Tukey Test given in descending order of magnitude.

recruitment rates, the nontraditional substrates used here can serve as suitable base materials for restoring oyster reefs if mounded to provide sufficient vertical relief. In low recruitment environments, however, it is important that adequate interstitial space be present to support oyster survival. In the present study, only oyster shells provided adequate interstitial space for the development of an oyster population in low recruitment years. Given our initial concern that oyster shells are in short supply throughout much of the mid-Atlantic region of the U.S. and the unpredictable nature of recruitment in many areas, we are led to ask how to best use available substrates for reef restoration. Repeated handling of surfclam shells—from the shucking house to reef construction—seems assured of resulting in fragmentation and the tight packing on reefs described above. Mixed shell plantings using surfclam shells in combination with other shell (e.g., whelks and hard clams) may support better development of oysters by reducing compaction and increasing available interstitial space (J. Wesson, Virginia Marine Resources Commission, pers. comm). Improved quality control in the production process of coal ash pellets could result in more uniform-sized pellets, similar to those used by Andrews et al. (1997), which had a mean diameter ≈ 5 cm, provided greater interstitial space, and supported good oyster survival. Perhaps the greatest impediment to the use of coal-ash pellets in future oyster reef restoration efforts results from the U.S. Federal Highway Act of 1995, which mandated the use of recycled material in roadbed construction; thereby, changing coal ash from a waste product into a commodity and increasing its cost.

A variety of alternative substrates for oyster settlement have been tested in other studies including slate (Haven et al. 1987), expanded shale, shredded tires (Mann et al. 1990), gypsum, *Rangia cuneata* shells, limestone, concrete, and gravel (Soniat et al. 1991, Haywood and Soniat 1992, Haywood et al. 1999). Varying degrees of suitability were observed for the different substrate types. In North Carolina, limestone marl is a routinely used settlement substrate in a fishery enhancement program (Marshall et al. 1999). The applicability of these substrates for large-scale endeavors may have to be re-evaluated in light of the findings presented in this study, particularly as they relate to substrate stability and interstitial volume.

The construction of reef structures in order to promote shellfish restoration represents a significant investment of public and private resources. Developing protocols that help maximize ecological return on this investment will be important for future efforts to restore oyster reef, as will evaluating these design and construction protocols on sufficiently large spatial and temporal scales. We have observed an interaction between the substrate used in the construction and oyster recruitment levels in the development of oyster populations on large-scale constructed reefs. During periods of low natural recruitment, only substrates that provide adequate interstitial space (oyster shell in the current study) are sufficient to support the development of a viable reef. During periods of high recruitment, poorer quality substrate (i.e., that providing less interstitial space) may prove sufficient as the newly recruited oysters themselves serve as ecosystem engineers (Jones et al. 1994) providing physical refuge. In temperate, polyhaline environments, the provision of vertical relief is important in ensuring oyster survival. Again, the combination of substrate placement and oyster recruitment, survival, and growth interact to affect restoration success. Therefore, restoration design criteria (e.g., the actual configuration of interstitial space and degree of vertical relief) must account for both geophysical (e.g., siltation and ice scour) and biological (e.g., subtidal and intertidal predators) mechanisms. Given these potential constraints, we appreciate that the many factors influencing oyster survival and growth, and hence a successful start to restoration efforts, have yet to be elucidated.

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