



Growth and mortality of oysters (*Crassostrea virginica*) on constructed intertidal reefs: effects of tidal height and substrate level

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Abstract

Intertidal oyster reefs, 3-dimensional structures created by years of successive settlement of larval oysters on adult oyster shells, provide levels of surface and interstitial heterogeneity that are rare in marine ecosystems. Surprisingly, little is known about the ecological benefits for oysters (*Crassostrea virginica*) in these aerially exposed, structurally complex systems. In this study a 210 m × 30 m intertidal reef was constructed. During three, 28-day sampling periods in the summer and early fall, growth and mortality of two size classes of oysters placed in cages at three tidal heights (25 cm above mean low water (MLW), MLW, and 90 cm below MLW) and at two substrate levels (reef surface and 10 cm below the reef surface) within the reef setting were examined. Mid-intertidal oysters residing within the reef interstices grew faster and enjoyed greater survival than mid-intertidal oysters at the reef surface during certain times of the year. Conversely, subtidal oysters inhabiting subsurface environments did not grow faster than surface dwelling subtidal oysters, but some oysters within the reef fabric (larger size class) experienced significantly higher survival. Along a tidal continuum, oysters at the reef surface grew best in subtidal locations, yet experienced the lowest mortalities in the low intertidal zone (MLW). Reef heterogeneity, which allows for residence along both interstitial and tidal gradients, may provide physical and biological refugia for oysters and furnish ideal spatial platforms for growth. Therefore, location within the reef habitat has a significant impact on the biology and ecology of *C. virginica*. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Physical and biological heterogeneity in the substratum increases the surface area available for settlement of marine organisms and provides refugia from predation and physical stresses. The plethora of microhabitats offered by topographically complex environments, like rocky intertidal habitats, reefs, or sea grass beds, are beneficial for the settlement/early colonization of barnacles (Crisp, 1974; Bergeron and Bourget, 1986; Bourget, 1988; Chabot and Bourget, 1988; Young, 1991; Anderson and Underwood, 1994), bivalves (Luckenbach, 1984; Bergeron and Bourget, 1986; Butman et al., 1988; Bourget et al., 1994; Bartol and Mann, 1997), polychaetes (Keough and Downes, 1982; Butman et al., 1988), coral (Rogers et al., 1984; Wallace, 1985; Babcock and Mundy, 1996), amphipods (Jacobi and Langevin, 1996), bryozoans (Walters, 1992), and fishes (Sale et al., 1984; Victor, 1986; Bortrone et al., 1994; Tolimieri, 1995). High rates of initial colonization within these microhabitats are often a product of preferential settlement, where larvae actively select topographically favorable features (Wetthey, 1986; Bergeron and Bourget, 1986; Keen, 1987; Chabot and Bourget, 1988; Crisp, 1990); hydrodynamic processes, where larvae are exposed to and/or entrained within microhabitats by flow patterns (Butman, 1987; Eckman, 1987; Wetthey et al., 1988; Snelgrove et al., 1993); or post-settlement processes, where early settlers experience less mortalities in these habitats than in less complex environments (Keough and Downes, 1982; Woodin, 1986).

After initial colonization, the type of microhabitat inhabited by marine organisms often plays a role in subsequent growth and survival. For example, spinyhead and roughhead blennies (*Acanthemblemaria spinosa* and *A. aspera*, respectively) that settle and inhabit coral reef hummocks grow significantly faster than blennies that settle in coral microhabitats that are 10s of cm lower in elevation because plankton, i.e. food, is more abundant near elevated reef surfaces (Clarke, 1992). Coral (*Platygyra sinensis*) larvae settling on various protuberances provided by adult coral grow faster than those that settle in shaded, protected environments because they are exposed to higher light levels (Babcock and Mundy, 1996). The oyster *Crassostrea rhizophorae* grows faster in mid-intertidal reef habitats than in low intertidal habitats that are several centimetres lower in elevation (Littlewood, 1988).

By providing refugia from predators, many microhabitats enhance survival. Clams (*Mercenaria mercenaria* and *Chione cancellata*) residing near seagrass stalks lower predation by whelks (Peterson, 1982), whereas other clams (*Tridacna gigas*) residing in coral reef habitats are cryptically protected from predators like fish (Lucas et al., 1989). Solitary ascidians (*Boltenia villosa* and *Styela gibbsii*) living as epizooites in structurally complex tunics of solitary ascidians (*Pyura haustor* and *Halocynthia igaboja*) reduce predation by the gastropod *Fusitriton oregonensis* relative to less complex habitats (Young, 1986), and sea urchins *Strongylocentrotus droebachiensis* residing in mussel beds reduce predation from crabs, lobsters, and fish (Witman, 1985). Amphipods, polychaetes, fish, and algae that inhabit structurally complex environments, such as rocky intertidal crevices or areas rich in macrophytes or worm tubes, also benefit from lower predation rates (Nelson, 1979; Woodin, 1981; Crowder and Cooper, 1982; Lubchenco, 1983).

Organisms inhabiting structurally complex environments reduce mortalities from physical stresses and competitors as well. Barnacles, such as *Balanus balanoides*, residing in crevices are less prone to dislodgment by waves (Connell, 1961), while *B. balanoides* living in mussel bed communities and gastropods inhabiting rocky intertidal depressions reduce mortality from thermal stress (Garrity, 1984; Stephens and Bertness, 1991). Survival of newly attached furoid *Pelvetia fastigiata* embryos is higher inside of algal canopies in the intertidal zone than on bare rock that tends to heat up when aerially exposed (Brawley and Johnson, 1991). When attaching to substrates 1.6 mm higher in elevation, the bryozoan *Electra* outcompetes the bryozoan *Alcyonidium*, which dominates when both organisms co-exist on level surfaces (Walters and Wethey, 1986). Similarly, when the bryozoan *Bugula turrita* grows in high density, complex habitats it avoids confrontations with the bryozoan *Schizoporella errata*, whose heavily calcified zooids allow it to overgrow the more flexible *B. turrita* in less dense environments (Buss, 1979).

Although many organisms benefit from physical and biotic heterogeneity, few are capable of both generating topographic complexity and exploiting its advantages. Corals may be the most obvious example of such an organism in shallow seas. Colonies of bryozoans *Membranipora villosa* have regions of nonfeeding, degenerate individuals every few millimetres that act as excurrent chimneys and transport filtered water above and away from the entire colony, reducing colonywide refiltration (Cook, 1977; Lidgard, 1981). Furthermore, barnacles (*Balanus*) settling on vertically oriented substrates create habitats with significant relief that encourage settlement by other barnacles, but prevent byssal attachment by dominant competitors, such as *Mytilus* (Menge, 1976).

An excellent example of organisms that create and probably benefit from large-scale habitats rich in surface and interstitial heterogeneity are oysters (Ostreidae), especially the Eastern Oyster, *Crassostrea virginica*. Oyster larvae preferentially settle and physically attach (in large numbers) to the shells of adult oysters, creating 3-dimensional habitats composed of live oysters and shell that often protrude above the water surface at low tide. Surprisingly, we know very little about the ecological benefits for oysters residing in these aerially exposed, structurally complicated systems. Bahr and Lanier (1981) suggest that reef communities serve to buffer desiccation stress for oysters on intertidal reefs, but present little quantitative data on oyster survival. For subtidal reefs in the Neuse River estuary, North Carolina, USA, Lenihan and co-workers (Lenihan, 1996; Lenihan et al., 1996; Lenihan and Peterson, 1998) have clearly demonstrated that vertical position of the reef affects the survival, growth, and disease dynamics for oysters. Similar details have not been quantified directly for intertidal reefs. Moreover, the effects of habitat complexity provided by interstitial space on the population dynamics of oysters have not been addressed.

Plausible benefits of habitat complexity (by which we mean relief in the vertical dimension and interstitial space within the fabric of the oyster reef) include refugia from predation and moderation of physical stress. Similarly, topographic complexity benefits organisms in rocky intertidal systems, seagrass beds, and corals. With these potential benefits in mind, we constructed a 210 m × 30 m intertidal oyster reef and tested hypotheses related to the growth and mortality of the Eastern Oyster, *Crassostrea virginica*, situated at the reef surface and within the reef interstices at various locations

along a tidal continuum. Specifically, we tested the hypotheses that (1) vertical position on the reef ranging from subtidal to intertidal locations affects oyster growth and survival, and (2) position within the reef, surface vs. subsurface, affects oyster growth and survival. Since oysters experience high mortalities within 6 months of settlement (Michener and Kenny, 1991; Roegner and Mann, 1995), two size/age classes, one 5 weeks old and one ~1 year old, were considered for comparison. Our primary goal was to determine, within a heterogeneous reef system, if substrate and tidal elevation have effects on the growth and survival of either size class of *C. virginica* during three, 28-day sampling periods from June through September.

2. Methods

2.1. Study site

This study was conducted in the Piankatank River, a sub-estuary of the Chesapeake Bay located in Virginia, USA, at a site that once supported a highly productive natural intertidal reef system (Fig. 1). However, at the time of reef construction, the site contained only a remnant shell footprint of the natural preexisting reef. The Piankatank River is ideal for artificial reef construction because it supports a productive adult oyster population, has a high abundance of oyster larvae settlement (Morales-Alamo and Mann,

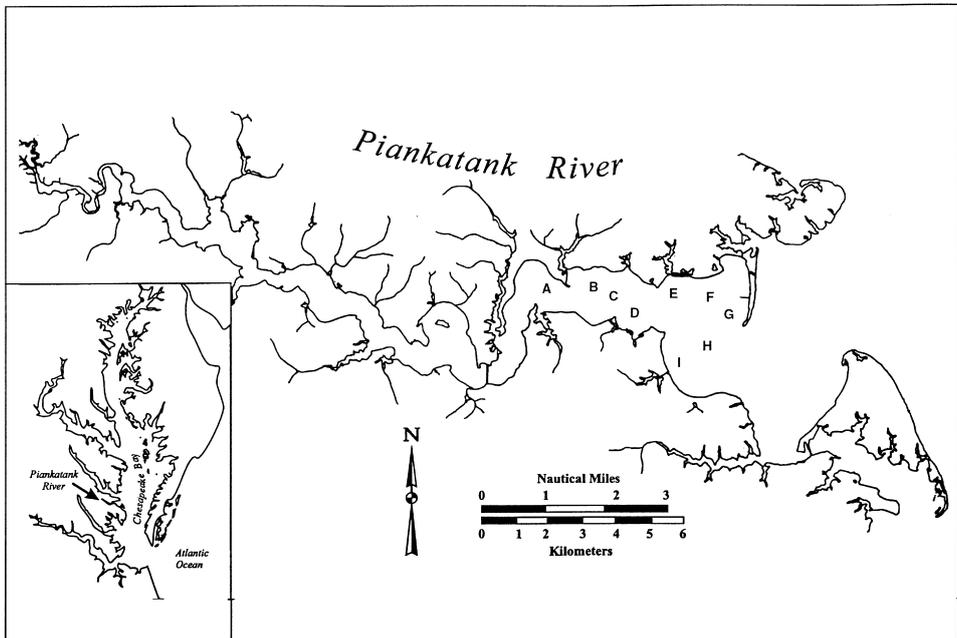


Fig. 1. Map of Piankatank River depicting the site of reef construction (D) and the location of other nearby reefs (A, B, C, E, F, G, H, I).

1997), and there is no commercial oyster fishery and virtually no industry or agricultural development within the watershed. Tidal range at this site is small (mean range = 0.36 m); however, local meteorological events, wind in particular, often dramatically alter this range by as much as 1.25 m. The site is relatively shallow (1–3 m), and consists of a sand and shell bottom. Throughout the year water temperature at the study site varies from 0.5–30°C, and salinity fluctuates from 8–20‰ (unpublished data recorded at Piankatank reef site: 1993–1996).

2.2. Reef construction

The Virginia Marine Resource Commission (VMRC) constructed the reef in June 1993. The construction procedure involved the deployment of aged oyster shells off barges using a high-pressure water cannon. The shells were broadcast on top of the preexisting footprint of the natural reef — an area ~210 m × 30 m. When this experiment was conducted, the reef consisted of ~30 semi-continuous, subtidal hummocks and eight distinct, aerially exposed hummocks varying in dimension from 9 to 40 m². Although the constructed reef ranged from 0.5 m above to 3.0 m below mean low water (MLW), most of the hummocks did not protrude higher than 0.35 m above MLW or extend deeper than 1.0 m below MLW.

2.3. Study design

All growth and mortality estimates were made using oysters spawned at the Virginia Institute of Marine Science (VIMS) Oyster Hatchery and deployed onto the reef. One cohort of oysters, spawned on July 22, 1993, was reared in flowing seawater tables for 3 weeks and then held in protected trays in the field for an additional 10 months before deployment on the reef. Oysters in this group had a mean shell area = 4.3 cm² (S.D. = 0.52) (see subsequent text for area measurement technique) and are referred to as the *Large* size class throughout the paper. A second cohort, spawned on May 16, 1994, was reared in the hatchery for a total of 5 weeks before deployment. This *Small* size class had a mean shell area of 1.18 cm² (S.D. = 0.10). Clean, disarticulated oyster shells were used as settlement substrate for competent larvae for both cohorts in the hatchery. Two size classes were considered because small juvenile oysters less than 6 months old typically experience high mortalities from physical and predatory stresses (Michener and Kenny, 1991; Roegner and Mann, 1995), while adults experience considerably lower mortalities (Shumway, 1996).

At the end of the 5-week and 11-month holding periods for the Small and Large size groups, respectively, we inspected the concave, smooth surface of the shells and chose shells which had 1–5 oysters for use in the experiment; the mean density per shell was 2.85 (S.D. = 0.37) for the Small group and 2.95 (S.D. = 0.48) for the Large group. Fifteen shells were haphazardly assigned to each of 48 groups for both size classes. Individual shells were labeled and the locations of 30 oysters, within each group of 15 shells, were mapped to facilitate repeated measures of the same oysters throughout the study. Care was taken to select oysters that were not initially confined by neighboring oysters and whose shell outlines were clearly visible in photographs.

Prior to deployment on the reef, the concave side of each labeled shell was photographed on slide film using a 35 mm Nikonos V camera equipped with a close-up lens and focusing frame. The (photographed) shell areas of 30 oysters in each group of 15 shells were calculated using an image analysis system manufactured by Biosonics Inc. (1992). These area measurements only represent the planer projected area of the upper valve of the oysters and not the entire shell surface area of the animal. After being photographed, the 15 shell units were placed on either the upper or lower level of labeled 32 cm \times 20 cm, three-tiered, 2.54 cm mesh cages. The upper and lower levels were 10 cm apart and separated by an intermediate level of 20 shells without oysters.

Tidal heights of 25 cm above MLW (mid-intertidal zone), MLW (low intertidal zone), and 90 cm below MLW (low subtidal zone) and eight aerially exposed hummocks were considered in the experimental design. The eight aerially exposed hummocks were partitioned into 64 cm \times 20 cm plots using rope and reinforced bars. All plots located at each of the three tidal elevations were grouped together, regardless of hummock, and eight independent plots were selected randomly at each tidal height for both the Small and Large size classes. The Small and Large class oyster cages were deployed at their designated plots on June 14 and June 20, 1994, respectively (1 day after being photographed). The cages were buried into the reef substrate until the upper layer of oysters was level with the reef surface and held in place with reinforced bars. No significant differences in initial densities were found for either size class across tidal heights and substrate levels (two-factor ANOVA (Small oysters): tidal height: $F = 0.074$, $df = 2,42$, $P = 0.940$; substrate level: $F = 0.41$, $df = 1,42$, $P = 0.513$; two-factor ANOVA (Large oysters): tidal height: $F = 0.181$, $df = 2,42$, $P = 0.672$; substrate level: $F = 0.507$, $df = 1,42$, $P = 0.606$). Furthermore, no significant differences in initial shell area were found for either size class across tidal height and substrate level (two-factor ANOVA (Small oysters): tidal height: $F = 0.071$, $df = 2,42$, $P = 0.792$; substrate level: $F = 0.041$, $df = 1,42$, $P = 0.908$; two-factor ANOVA (Large oysters): tidal height: $F = 0.945$, $df = 2,42$, $P = 0.397$; substrate level: $F = 0.695$, $df = 1,42$, $P = 0.409$).

At 28-day intervals in July, August, and September, cages were removed from their designated plots and opened. Numbers of flatworms, mud crabs, and blue crabs present at each level of the cages were recorded. Oysters were subsequently removed from the cages, cleaned using a 3 HP gasoline powered Homelite water pump, and photographed with the Nikonos V camera. Using the Biosonics image analysis system, growth values for oysters were computed using the equation: $G = (A_t - A_{t-1})/d$, where A is shell area (mm^2), t is sample interval (1–3), and d is the duration of the sampling interval (days). Mean growth values for each 15-shell assemblage were computed subsequently over all three, 28-day sampling intervals. For each 28-day sampling interval a mean proportional mortality value ($\#$ dead oysters at the end of the 28-day interval/ $\#$ live oysters at the beginning of the interval) also was computed for each 15-shell assemblage.

2.4. Physical parameters

Each week throughout the study, water temperature, air temperature, salinity, and Secchi disk readings were recorded at the reef site. Automated sensors, located on a VIMS pier in the York River, which is located \sim 32 km from the study site, also were

used to record air temperatures. To develop a relationship between surface and subsurface intertidal temperatures on the reefs, mercury thermometers were placed at the reef surface and 10 cm below the surface at the + 25 cm tidal elevation for 2 h during several sunny days from June through September.

2.5. Flow speed estimates

At the end of the oyster growth and survival portion of this study we determined *relative* time-averaged flow speeds at all plots considered in this study using dissolution rates of chlorine tablets over 48-h periods. Dissolution rates of other materials (primarily gypsum) have been used by other investigators (e.g. Doty, 1971) to estimate flow rates; however, these materials often give unreliable results for time periods greater than a few hours because they become pitted and pieces break off. We have found that 3-inch diameter chlorine tablets, commercially available for swimming pool disinfection, provide a reliable and repeatable means of obtaining dissolution rates in the field over time scales of hours to days.

Though relative flow rates suffice for the comparisons made between sites here, the chlorine tablets have been calibrated to determine the relationship between dissolution rate and actual flow speed under a variety of conditions (Luckenbach, unpublished data). For clarification, we report the relevant part of those calibration data here. Calibration of tablets was conducted in a 5-m long recirculating seawater flume. The flume, which has been described in detail in Orth et al. (1994), permits control of flow speed and water temperature. The flume was filled with 20 ppt seawater, the water temperature was adjusted to 20°C, and the free-stream velocity was set to one of five levels: 5, 10, 15, 20 and 25 cm s⁻¹. Three pre-weighed, replicate tablets were suspended above the flume bed in mesh bags for up to 20 h in slow flows and 5 h at the two highest flows. Pellets were retrieved, blotted dry, and weighed at intervals throughout the period. The total length of time and the intervals between weighing varied to permit comparison of dissolution rates at equal flux levels (e.g. 10 h at 10 cm s⁻¹ vs. 5 h at 20 cm s⁻¹). Dissolution rates at each flow speed were computed as weight loss/h within each interval.

Dissolution rates of chlorine tablets varied linearly with flow speed in the flume calibration runs (Fig. 2). There was no visual evidence of pitting or breakage among pellets used in the flume or the field. Thus, we believe that these pellets serve as a reasonable surrogate measure for time averaged flow speeds in the field. They do not, however, provide any information about flow direction or the time variance in flow speeds throughout the deployment; nor do we know how oscillatory flow and turbulence intensity affect the rates of dissolution. Further, they sublime and lose weight during air exposure at a rate that is a partial function of molecular and turbulent diffusion in air. Nevertheless, for the purpose employed here, they provide reliable estimates of relative flow speeds at various plots within a tidal height on the reef.

2.6. Statistical analysis

Although the data fit nicely into a split plot/repeated measures analysis of variance (ANOVA) model with one between factor (tidal height) and two within factors (time and

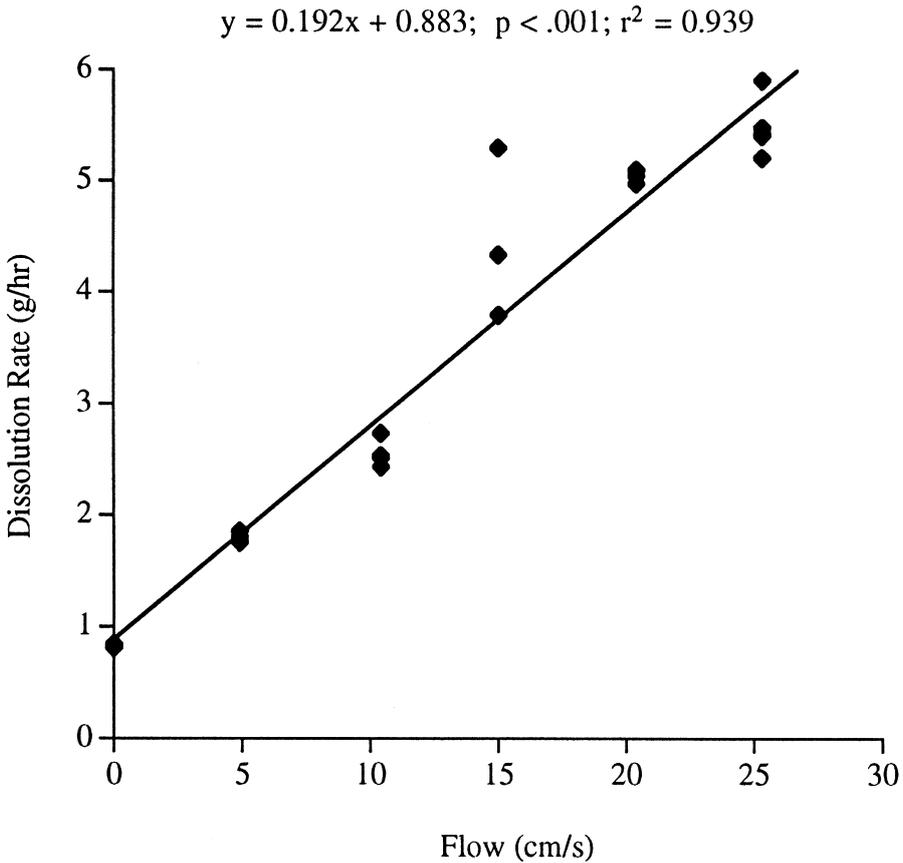


Fig. 2. Linear regression of chlorine tablet dissolution rate on flow speed.

substrate level), interactions between plots and within factors violated the assumptions of this design and precluded its use (Winer et al., 1991; Zar, 1996). Therefore, for each size class, we opted to randomly select four plots at each of the three tidal elevations, and at these plots, use only surface growth/mortality values. For the remaining four plots within each tidal elevation, we considered only deep samples. This reduced the sample size, but allowed for the treatment of substrate level as a fixed factor in subsequent models.

Three factor repeated measures ANOVAs with two between factors (tidal height and substrate level) and one within factor (time) were used to analyze the data. Analyses were performed separately by size class on growth and mortality data. Both size classes were not analyzed together in statistical models because different sampling dates were considered for the Large and Small oysters (this was necessary because of sampling time constraints). Tests for homogeneity of both the between- and within-subjects sources of variation revealed heterogeneity in growth and mortality data (Winer et al., 1991; pp. 543–546). Thus, growth data were log transformed and mortality data were arcsine

transformed to homogenize the variances. Student-Newman-Keuls *a posteriori* tests were used to explore differences among means when significant factor and interactive effects were detected (Winer et al., 1991; pp. 526–528).

Linear regressions of log transformed growth on dissolution rate were performed to determine if a functional dependence was implied. Analyses were performed separately by each year class, substrate level position, and tidal elevation. Since surface and deep level values were analyzed separately, dissolution rates and growth measurements at all eight plots at each tidal elevation were considered in the regression analyses. The assumptions of the regressions were met as determined by residual analysis (Zar, 1996).

3. Results

3.1. Growth

3.1.1. Large oysters

A significant tidal height \times substrate level interaction ($P < 0.05$) was detected for the growth of Large oysters (Table 1). At +25 cm growth was greater 10 cm below the surface than at the surface, and at -90 cm growth was greater at the surface than below (Fig. 3). Further SNK tests revealed that oysters residing at the surface grew faster at -90 cm and MLW than at +25 cm, but no difference in growth at MLW and -90 cm was detected (Fig. 3). No growth differences at the three tidal elevations were observed beneath the reef surface.

There was a significant effect of time on Large oyster growth (Table 1). Oysters situated at both substrate levels grew fastest during the August/September sampling period, irrespective of tidal elevation (Fig. 4). Furthermore, oysters situated at -90 cm experienced a visible decrease in growth during the July/August sampling period, although this decline was not significant at the $\alpha = 0.05$ level (Table 1: time \times tidal height = 0.617; Fig. 5).

Table 1
Multivariate repeated measures ANOVA of growth data from the Large size class of oysters

Source	df	SS	MS	F-value	P-value
Tidal height	2	101.123	50.562	13.159	0.0003
Substrate level	1	0.839	0.839	0.218	0.6460
Tidal height \times substrate level	2	52.433	26.216	6.823	0.0062
Subject (group)	18	69.164	3.842		
Time	2	195.721	97.861	48.450	<0.0001
Time \times tidal height	4	19.988	4.997	2.474	0.0617
Time \times substrate level	2	10.242	5.121	2.535	0.0933
Time \times tidal height \times substrate level	4	14.275	3.569	1.767	0.1570
Time \times subject (group)	36	72.713	2.020		

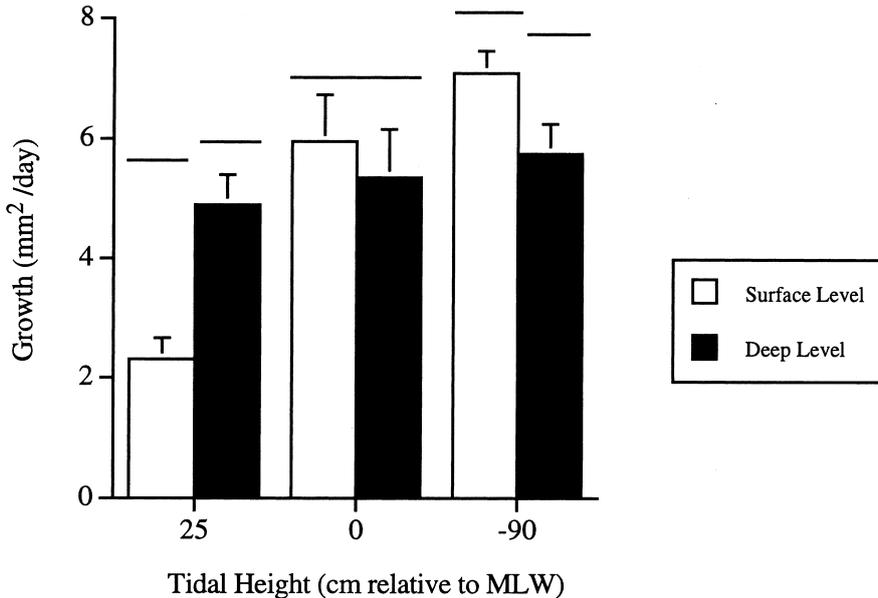


Fig. 3. Mean surface and subsurface (deep) growth rates of Large oysters residing at the three tidal elevations. Broken lines above the bars represent significant differences between surface and deep values. Other SNK tests (not depicted directly in the figure) revealed that oysters residing at the surface grew faster at -90 cm and MLW than at $+25$ cm, but no significant difference in growth at MLW and -90 cm was detected. Beneath the reef surface, no growth differences at the tidal heights were detected. All error bars denote $+1$ S.E.

3.1.2. Small oysters

A significant tidal height \times substrate level interaction ($P < 0.05$) was detected when growth data from Small oysters were analyzed (Table 2). As was the case with Large oysters, Small oysters at $+25$ cm grew faster below the surface than at the surface, whereas Small oysters at -90 cm grew faster at the surface than below (Fig. 6). At the reef surface, oyster growth increased with tidal depth, but no significant differences in growth rates were detected beneath the reef surface (Fig. 6).

A time \times tidal height interaction also had a significant effect on Small oyster growth (Table 2). SNK tests performed to decouple the cause of the time \times tidal height interaction revealed: (1) during the June/July period growth at -90 cm and MLW was greater than growth at $+25$ cm; (2) during the July/August period no difference in growth according to tidal height was detected; and (3) during the August/September period, growth at -90 cm was greater than that at $+25$ cm and MLW (Fig. 7). The lack of growth differences at the various tidal elevations during the July/August period was a product of a significant decline in growth at MLW and -90 cm (when compared to growth during the June/July and August/September periods). Furthermore, growth was high during the August/September period for all tidal heights, especially at $+25$

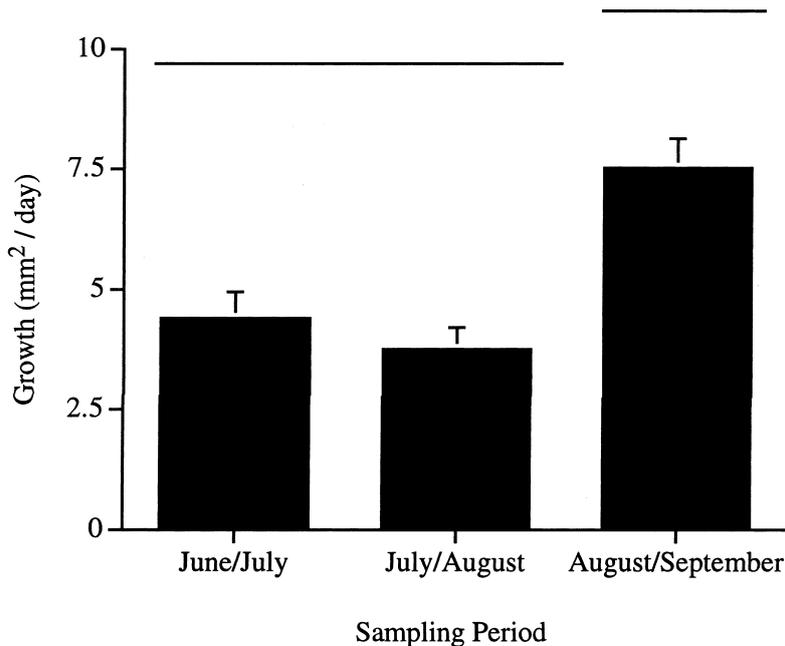


Fig. 4. Mean growth rates of Large oysters during the three sampling periods. Lines above bars represent the results of SNK tests. All bars denote + 1 S.E.

cm and -90 cm, where growth increased significantly relative to the preceding periods (Fig. 7).

3.2. Mortality

3.2.1. Large oysters

A significant time \times tidal height \times substrate level interaction ($P < 0.05$) was detected in the mortality data from Large oysters (Table 3). SNK tests revealed that throughout the sampling period, oysters at -90 cm experienced significantly lower mortality below the surface than at the surface. Oysters at $+25$ cm had significantly lower mortality below than at the surface as well, but only during the June/July period. Conversely, oysters at MLW had significantly lower mortality at the surface than below during the August/September period. These differences were manifested in cumulative mortality values recorded at the end of the study (Fig. 8). Of the oysters that resided at the surface, those that were situated at MLW had significantly lower mortality than those at $+25$ cm and -90 cm during the June/July and August/September periods (Fig. 9). During the July/August period mortality at MLW was lower than that at $+25$ cm but not that at -90 cm. No differences in mortality by tidal height were detected for oysters residing

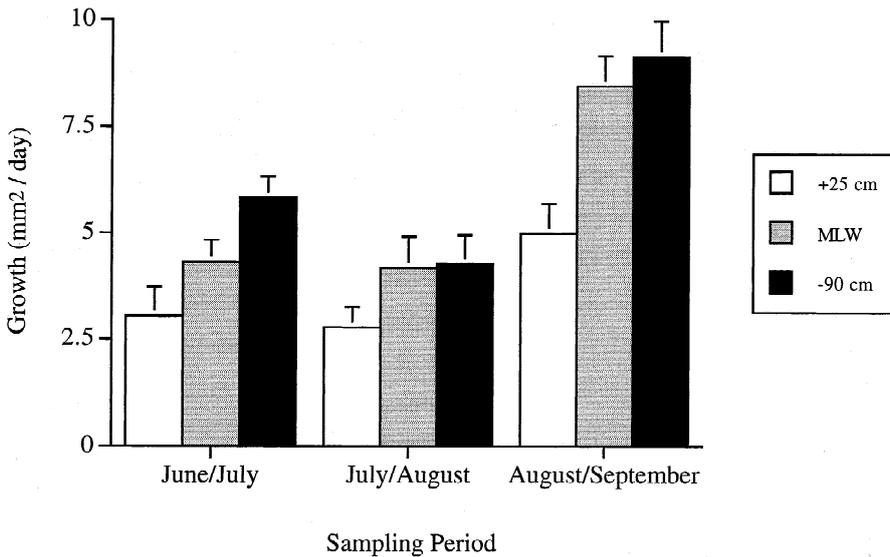


Fig. 5. Mean growth rates of Large oysters residing at three tidal elevations during the three sampling periods. Note the trend in reduced growth at -90 cm during the July/August sampling period. All error bars denote $+1$ S.E.

below the surface. Finally, for oysters residing at the surface within the subtidal zone (-90 cm), mortality was greatest during the August/September period (Fig. 9).

3.2.2. Small oysters

A significant time \times tidal height interaction ($P = 0.0047$) and a nearly significant time \times tidal height \times substrate level interaction ($P = 0.0683$) were detected for mortality data from the Small size class (Table 4). The low P -value in the three-way interaction was in part a product of higher surface (40.2%; S.D. = 10.3) than below surface (8.4%; S.D. = 5.7) mortality at the $+25$ cm tidal height during the June/July period. SNK tests performed to decouple the time \times tidal height interaction revealed: (1) during the

Table 2
Multivariate repeated measures ANOVA of growth data from the Small size class of oysters

Source	df	SS	MS	F-value	P-value
Tidal height	2	86.066	43.033	19.639	< 0.0001
Substrate level	1	2.163	2.163	0.987	0.3336
Tidal height \times substrate level	2	24.529	12.264	5.597	0.0129
Subject (group)	18	39.441	2.191		
Time	2	108.573	54.286	30.006	< 0.0001
Time \times tidal height	4	30.05	7.512	4.152	0.0072
Time \times substrate level	2	6.813	3.407	1.883	0.1668
Time \times tidal height \times substrate level	4	5.456	1.364	0.754	0.5621
Time \times subject (group)	36	65.130	1.809		

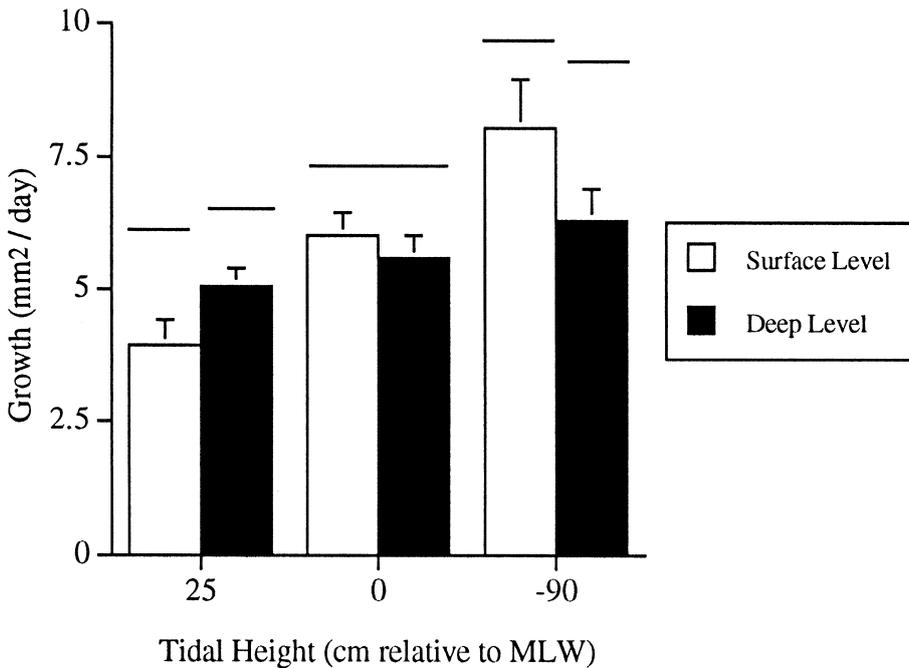


Fig. 6. Mean surface and subsurface (deep) growth rates of Small oysters residing at the three tidal elevations. Broken lines above bars represent significant differences between surface and deep values. Additional SNK tests (not depicted directly in the figure) revealed that oysters at the surface grew faster at -90 cm than at MLW, and oysters at MLW grew faster than those at $+25$ cm. All error bars denote $+1$ S.E.

June/July period mortality was highest at $+25$ cm; (2) during the July/August period mortality was highest at -90 cm; and (3) during the August/September period mortality was significantly lower at $+25$ cm than at -90 cm, but there was no detectable difference between mortality at MLW and at either $+25$ cm or -90 cm (Fig. 10). Cumulative mortalities recorded at the end of the experiment were lowest at the MLW tidal height (Fig. 11). Overall mean cumulative mortality ranged from 40.0 to 75.3% which was higher than that documented for the Large oysters, which varied from 10.3 to 34.7%.

3.3. Physical and biological factors

Dissolution rates were greatest at the reef crests and lowest at the reef bases, and within each tidal elevation, there was a general lack of linear dependence of growth on dissolution rate for either size class (Table 5). Large oysters residing at the reef surface at -90 cm were the only oysters that demonstrated a significant linear relationship between growth and dissolution rate. Interestingly, overall trends (i.e. a positive or negative slope) in growth as a function of dissolution rate were inconsistent as well (Table 5), and no hyperbolic relationships between growth and dissolution that would

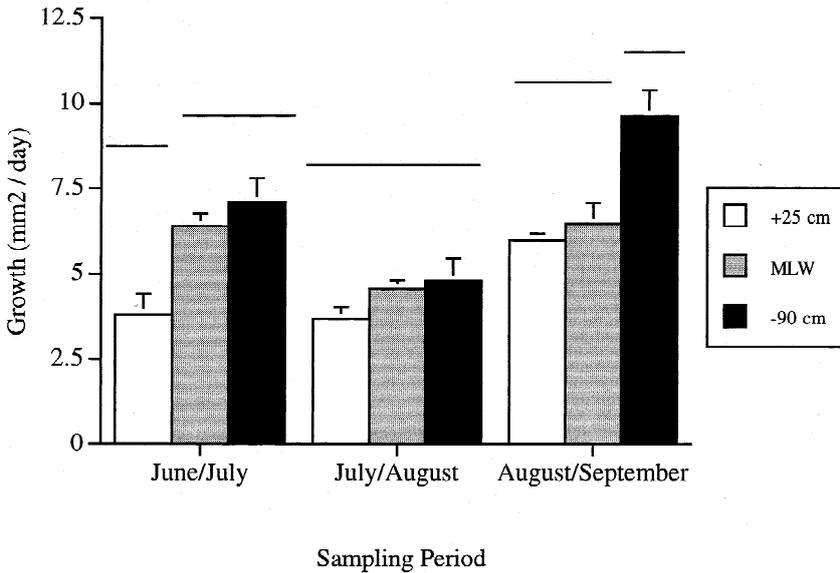


Fig. 7. Mean growth of Small oysters residing at three tidal elevations during the three sampling periods. Lines above bars represent results of SNK tests performed within each sampling period. Results of additional SNK tests (not depicted directly in the figure) revealed that growth was lowest during the July/August period for oysters at MLW and -90 cm and was highest during the August/September period for oysters at $+25$ cm and -90 cm. All error bars denote $+1$ S.E.

suggest an optimal velocity range were observed. Salinity, water temperature, and Secchi disk readings recorded during the sampling periods are presented graphically in Fig. 12. During the first sampling period, which began June 14 for Large oysters and June 20 for Small oysters, there was a rapid increase in salinity. Salinity in subsequent periods, however, was relatively constant, fluctuating between only 15‰ and 17‰. Water temperatures during the first two sampling periods (mid June–mid July and mid July–mid August) ranged from 26–30°C, and during the last sampling period (mid August–mid September) were consistently lower (22.5–27°C). Water clarity also

Table 3
Multivariate repeated measures ANOVA of mortality data from the Large size class of oysters

Source	df	SS	MS	F-value	P-value
Tidal height	2	838.012	419.006	17.411	< 0.0001
Substrate level	1	47.515	47.515	1.974	0.1770
Tidal height \times substrate level	2	477.400	238.700	9.919	0.0012
Subject (group)	18	433.170	24.065		
Time	2	411.645	205.823	7.282	0.0022
Time \times tidal height	4	566.084	141.521	5.007	0.0026
Time \times substrate level	2	46.040	23.020	0.814	0.4509
Time \times tidal height \times substrate level	4	468.858	117.215	4.147	0.0073
Time \times subject (group)	36	1017.499	28.264		

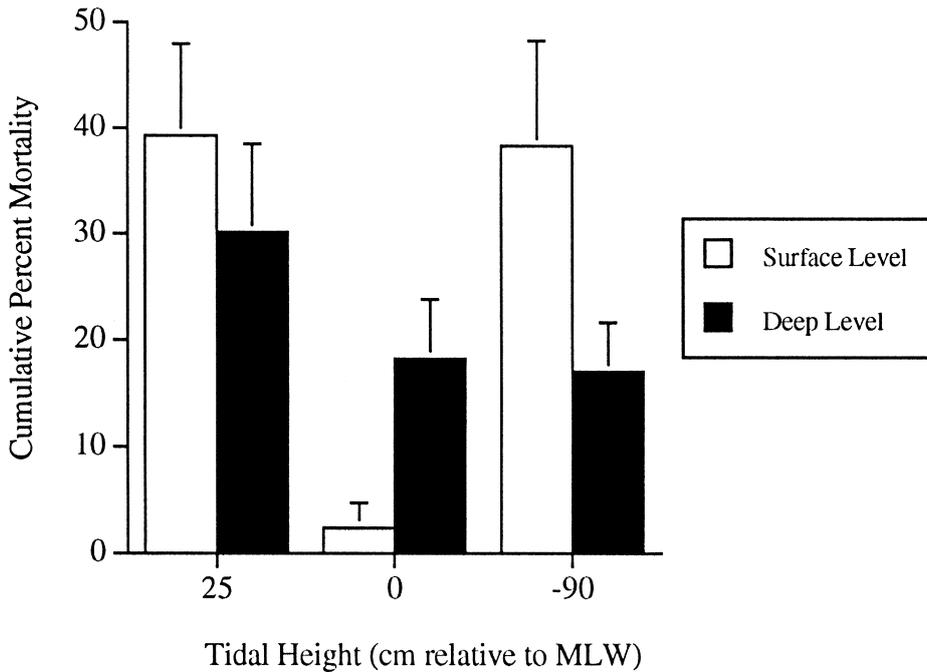


Fig. 8. Mean cumulative percent mortalities of Large oysters residing at and beneath the reef surface at the three tidal elevations. All error bars denote +1 S.E.

improved during the last sampling period, which began August 9 for Large oysters and August 16 for Small oysters. Furthermore, mean air temperatures were greatest during the June/July period (Large oyster study: 28.0°C (S.D. = 5.6); Small oyster study: 28.2°C (S.D. = 4.1)) and lowest during the August/September period (Large oyster study: 25.1°C (S.D. = 2.6); Small oyster study: 24.3°C (S.D. = 3.2)) for both year classes. Based on four measurements in the field throughout this study, air temperatures were 9–17°C lower 10 cm below the reef surface than at the surface at +25 cm. Furthermore, based on field observations, conditions were substantially moister within underlying reef layers than at the reef surface within the intertidal zone.

Although no measurements were made to quantify the effects of predation, a number of potential predators were observed within the oyster cages. The most prevalent predators were the flatworm *Stylochus ellipticus*, the mud crabs *Panopeus herbstii*, *Eurypanopeus depressus*, and *Rhithropanopeus harrisi*, and the blue crab *Callinectes sapidus*. These predators were clearly most abundant in the upper level of subtidal (–90 cm) cages (Fig. 13).

4. Discussion

Intertidal oyster reefs, complex 3-dimensional structures formed by the successive

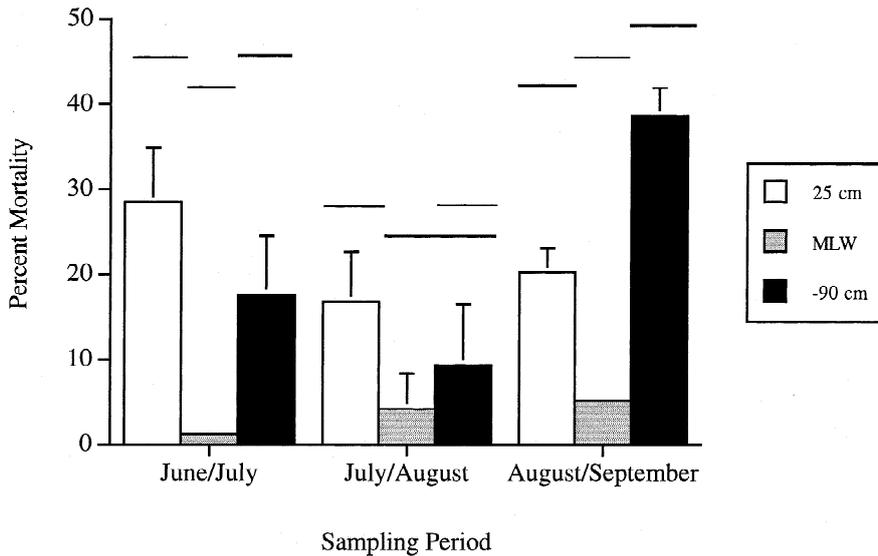


Fig. 9. Mean percent mortalities for surface-residing Large oysters situated at the three tidal elevations during the three sampling periods. Lines above bars represent results of SNK tests performed within each sampling period. Lines either connecting or at the same altitude as other treatments do not differ at $\alpha = 0.05$. Additional SNK tests (not depicted directly in the figure) revealed that for surface-residing, subtidal (-90 cm) oysters, mortality was greatest during the August/September period. All error bars denote $+1$ S.E.

settlement of generations of oysters, provide suites of habitat along both tidal and interstitial continuums. The results of this study suggest that position within these continuums strongly influences growth and mortality processes in *C. virginica*. Both small (~ 1 cm²) and large (~ 4 cm²) oysters living in the mid-intertidal zone ($+25$ cm) grew faster within the reef interstices than at the reef surface, whereas oysters living in the subtidal zone (-90 cm) grew faster at the reef surface than within the reef interstices. Large oysters experienced lower subsurface than surface mortality at -90 cm throughout the study and at $+25$ cm during the June/July sampling period. There was also some evidence to suggest that small oysters living within the reef interstices at

Table 4
Multivariate repeated measures ANOVA of mortality data from the Small size class of oysters

Source	df	SS	MS	F-value	P-value
Tidal height	2	433.716	216.858	3.293	0.0604
Substrate level	1	197.044	197.044	2.992	0.1008
Tidal height \times substrate level	2	270.797	135.398	2.056	0.1569
Subject (group)	18	1185.264	65.848		
Time	2	906.432	453.216	10.064	0.0003
Time \times tidal height	4	812.171	203.043	4.509	0.0047
Time \times substrate level	2	243.206	121.603	2.700	0.1083
Time \times tidal height \times substrate level	4	417.068	104.267	2.396	0.0683
Time \times subject (group)	36	1621.184	45.033		

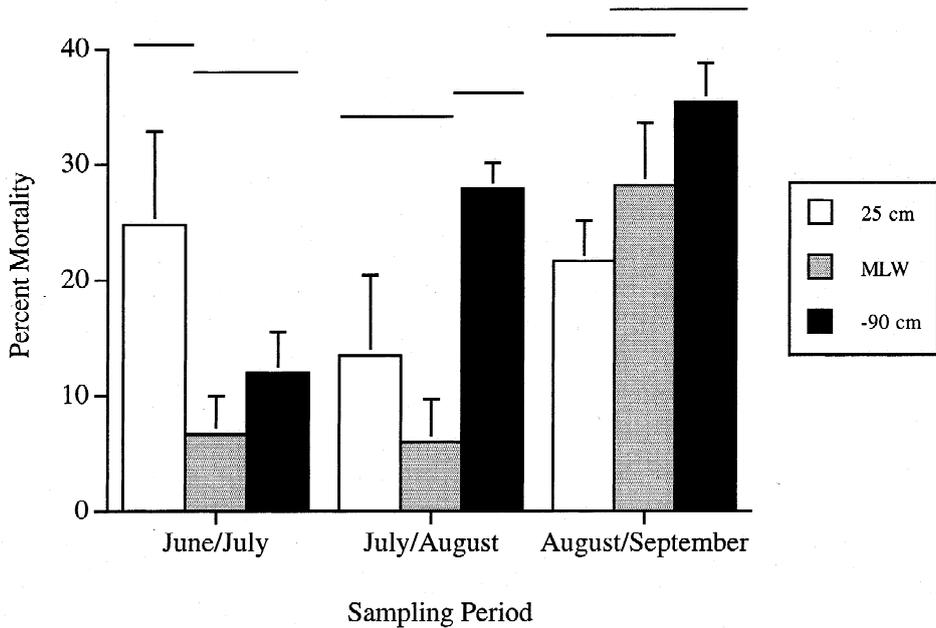


Fig. 10. Mean percent mortalities for Small oysters situated at three tidal elevations during the three sampling periods. Lines above bars represent results of SNK tests performed within each sampling period. All error bars denote +1 S.E.

+ 25 cm benefited from lower mortality than oysters residing at the surface during the June/July period, though there was no evidence to suggest that subsurface residence was advantageous for small oysters at -90 cm. Both size classes of oysters residing at the surface grew faster in the subtidal zone (-90 cm) than in the mid-intertidal zone (+25 cm). No consistent growth differences between subtidal and low intertidal (MLW) heights were detected at the surface, however, and no differences in growth by tidal elevation were detected for oysters residing within the reef interstices. At the reef surface, both sizes of oysters survived best at MLW. Furthermore, oysters generally grew fastest during the August/September period — a period when subtidal (-90 cm) mortalities were high.

Interstitial residence is particularly advantageous for oysters in the mid-intertidal zone. Subsurface intertidal environments tend to be lower in vertical elevation than those at the reef surface and are inundated longer by tidal flow, allowing oysters residing there to filter feed for longer periods than oysters at the reef surface. The attainment of larger size in *C. virginica* with increased submergence time has been demonstrated by Loosanoff (1932), Ingle and Dawson (1952), Burrell (1982), and Roegner and Mann (1995). Elevated growth within interstitial, intertidal habitats also may have been a consequence of reduced metabolic stress. In this study intertidal air temperatures were 9–17°C less 10 cm below the reef than at the surface during several sunny days in June, August, and September. Similarly, Bahr (1976) found temperatures 6 cm beneath the surface at an intertidal oyster reef community at Sapelo Island, Georgia, to be 7°C lower than that at the surface in October. Intertidal oysters exposed to physical stresses, like

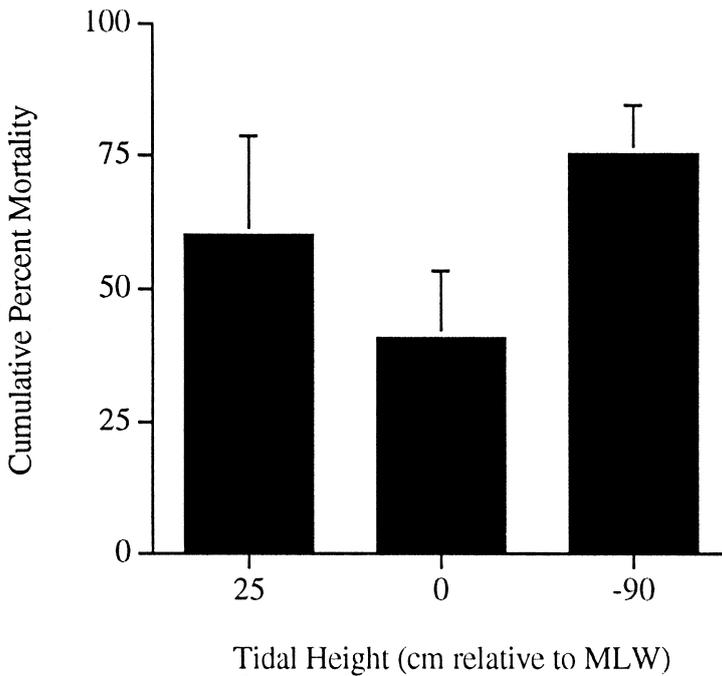


Fig. 11. Mean cumulative percent mortalities of Small oysters residing at three tidal elevations. Error bars denote +1 S.E.

high temperatures, allocate more energy to metabolic maintenance, and this reduces the amount of energy available for somatic growth (Dame, 1972; Newell, 1979). Subsurface intertidal oysters resided in a cooler, moister environment than oysters at the surface and thus presumably could appropriate more energy for growth.

Table 5

Results from regressions of oyster growth on chlorine tablet dissolution rate. Analyses were performed separately by tidal elevation, size class, and substrate level. Asterisks (*) denote significance at the $\alpha < 0.05$ level

Tidal elevation	Size class	Substrate level	Slope	P-value	r^2
+ 25 cm	Small	Surface	-0.018	0.667	0.033
		Deep	0.097	0.145	0.319
	Large	Surface	0.072	0.219	0.239
		Deep	0.063	0.146	0.203
MLW	Small	Surface	-0.017	0.426	0.108
		Deep	-0.013	0.425	0.109
	Large	Surface	0.007	0.915	0.002
		Deep	0.013	0.708	0.025
- 90 cm	Small	Surface	0.016	0.807	0.011
		Deep	-0.040	0.345	0.149
	Large	Surface	0.057	<0.001*	0.865
		Deep	-0.032	0.341	0.151

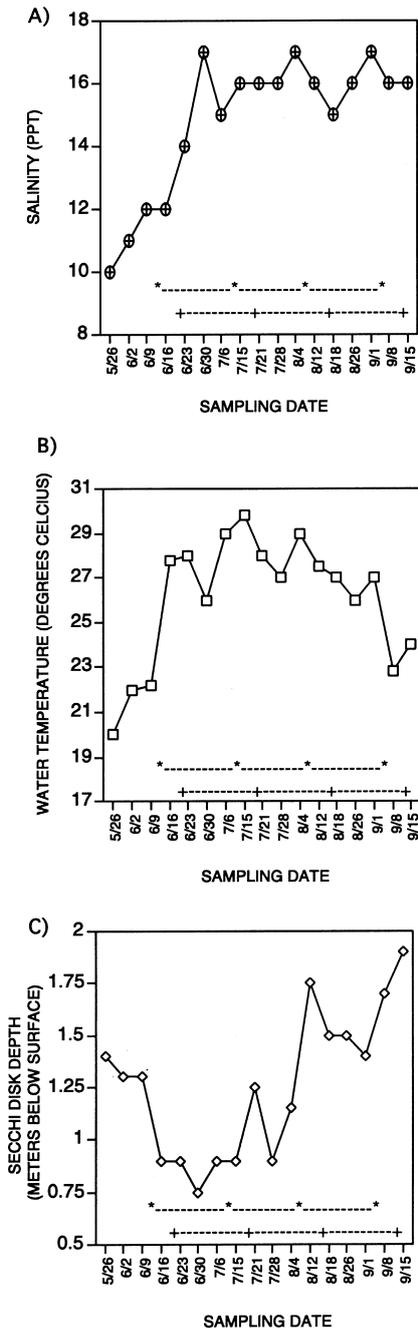


Fig. 12. Salinity, water temperature, and Secchi disk readings recorded during the sampling period. Sampling intervals for the Large and Small oysters are denoted by the symbols (*) and (+), respectively.

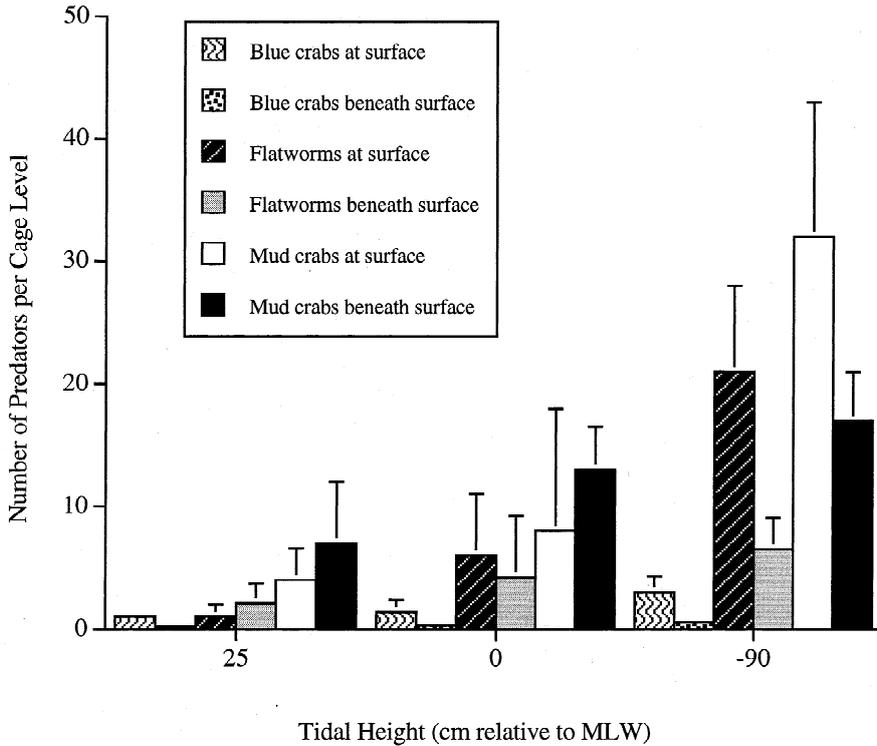


Fig. 13. Mean number of flatworms, mud crabs, and blue crabs found within surface and subsurface cage levels at the three tidal elevations. The data from both Small and Large oyster cages are pooled. Error bars denote +1 S.E.

Residence within the reef interstices also was beneficial for survival of intertidal oysters during the June/July period — the sampling interval with the highest mean air temperature (28.2°C) and when temperatures occasionally rose to 37°C. Adult oysters are capable of tolerating intertidal temperatures of 46–49.5°C for short periods (hours) (Galtsoff, 1964; Ingle et al., 1971), but when subjected to lower temperatures (e.g. 35°C) for longer periods (days), they experience significant mortality (Quick, 1971). Juveniles may have even lower thermal limits. In Virginia from June through early August when air temperatures were above 30°C, Roegner and Mann (1995) found 100% mortality rates for juvenile oysters set on plates at intertidal levels of 25 cm, 50 cm, and 75 cm above MLW. Similarly, in South Carolina, Crosby et al. (1991) reported summer intertidal cumulative mortalities of 79% for young oysters set on exposed asbestos plates. Although extensive physical data from surface and subsurface environments were not collected, the limited data presented in this study suggest that temperatures within the reef interstices were cooler and moister than at the surface. Therefore, it is reasonable to assume that oysters in underlying environments may have benefited from reduced environmental stress, which is extremely advantageous in the intertidal zone. In other intertidal environments, physical structure (e.g. crevices, rocky hummocks) and

other organisms provide important refugia from heat and desiccative stress for marine organisms and elevate survival (Garrity, 1984; Underwood and Denley, 1984; Stephens and Bertness, 1991; Brawley and Johnson, 1991).

The lack of growth benefits for subsurface, subtidal residence was not surprising given that oysters in these environments did not benefit from longer submergence times (both subtidal environments were submerged constantly) and more favorable environmental conditions (there was no difference in refugia from atmospheric stress) like subsurface, intertidal oysters. Interestingly, large oysters experienced greater survival below the reef surface than at the surface within the subtidal zone throughout the study. This may have been in part because subsurface substrate provided a refuge from predation. Flatworms, *Stylochus ellipticus*, which may cause oyster mortalities as high as 50% (Hopkins, 1955; Mackin, 1959; Landers and Rhodes, 1970; MacKenzie, 1981; Abbe, 1986; Littlewood, 1988; Morales-Alamos et al., 1988; Baker, 1994), mud crabs *Panopeus herbstii*, *Eurypanopeus depressus*, and *Rhithropanopeus harrisi*, which may prey upon oysters as large as 25 mm in shell height (Abbe, 1986; Bisker and Castagna, 1987; Baker, 1994); and blue crab *Callinectes sapidus*, which prey upon oysters of all sizes (Hofstetter, 1977; Kranz and Chamberlain, 1978; Abbe, 1986; Bisker and Castagna, 1987; Roegner, 1989; Eggleston, 1990a,b,c) were all abundant in the subtidal zone, but were less prevalent in subsurface than surface cage levels. Although the effects of predation were not measured directly in this study, lower numbers of potential predators in interstitial, subtidal environments suggest that predation may have been less significant in these subsurface environments.

Lower numbers of predators were found within the lower tier of cages holding small oysters as well, yet there was no detectable difference in surface/subsurface mortality. Sedimentation, a major source of mortality in small oysters (MacKenzie, 1981; Abbe, 1986), and hypoxia, which requires oysters to switch from aerobic to anaerobic metabolism — something that is difficult for small oysters because of limited glycogen reserves (Galtsoff, 1964; Holland and Spencer, 1973) — are more problematic in underlying layers of reef communities (Bahr and Lanier, 1981) and together may have eliminated the predatory benefits of subsurface residence. During reproductive periods in adult oysters, glycogen reserves are shifted from muscles to gametes, which lowers their ability to tolerate hypoxic conditions as well (Barber et al., 1988a,b; Thompson et al., 1996). Though subsurface mortalities of Large oysters were not particularly high, the synergistic effects of both sedimentation and hypoxia may be responsible for the high subsurface mortalities observed in the Small oysters.

Oyster growth in relation to tidal height is quantified in several studies, most of which suggest that organisms situated in the subtidal zone will experience greater growth than organisms situated at mid and high intertidal heights. Loosanoff (1932), Ingle and Dawson (1952), Burrell (1982), and Roegner and Mann (1995) all found greater growth for *C. virginica* situated in the subtidal zone than in the mid/high intertidal zone, and Sumner (1981) and Walne (1958) found similar results for *Crassostrea gigas* and *Ostrea edulis*, respectively. Crosby et al. (1991) examined recently settled (1–14 d) *C. virginica* for eleven weeks and determined that subtidal oysters have greater cumulative and periodic growth rates than intertidal (20% aerial exposure) oysters during the first 52–55 days post-settlement, when intertidal and subtidal immersion times are ≤ 850 h and ≤ 1320 h, respectively. However, between ~ 55 and 77 days when total post-settlement

immersion times of intertidal and subtidal oysters are ~ 900 – 1330 h and ~ 1320 – 1870 h, respectively, cumulative growth rates of intertidal and subtidal oysters no longer differ and periodic growth of intertidal oysters may even be greater than that of subtidal oysters. Crosby et al. suggested that this occurs because subtidal oysters reach a genetically pre-determined size where shell growth decreases and tissue growth increases, allowing intertidal oysters, which take longer to reach this size because of reduced immersion times, to catch up with subtidal oysters during early development. Interestingly, Gillmor (1982) presented evidence that juvenile *C. virginica* held in the intertidal zone under certain levels of aerial exposure ($\sim 20\%$) are capable of faster growth than subtidal oysters because they have the ability to supplement energy input during periodic aerial exposure. Conversely, Littlewood (1988), working with *C. rhizophorae* in Jamaica, was unable to detect a significant difference in growth between oysters in the mid-intertidal and subtidal zones.

There are no studies that show conclusively that oysters situated in the subtidal zone experience faster growth than oysters in the low intertidal zone. Spencer and Gough (1978) were unable to detect a difference in growth of either *C. gigas* or *O. edulis* held subtidally and in the low intertidal zone. Littlewood (1988) found that oysters in the low intertidal zone (1–3% aerial exposure) exhibit some growth reduction relative to oysters in the mid-intertidal zone (17% aerial exposure), but detected no growth differences between oysters in the low intertidal zone and in the subtidal zone. Roegner and Mann (1995) demonstrated that during the spring *C. virginica* growth at MLW was about 50% less than that at -75 cm, but during the summer and fall, no such consistent differences were observed. Roegner and Mann concluded that there was no evidence for the negative effects of aerial exposure on oyster growth in the low intertidal zone.

The results of this study suggest that at the reef surface oyster growth rates are greater at subtidal locations than in the mid-intertidal zone, but that no consistent growth differences are present when oysters in subtidal and low intertidal (MLW) heights are compared. Therefore, longer periods of submergence are beneficial to a point, in that they allow for longer durations of feeding, but growth is not simply a direct function of submergence time. This was demonstrated by Crosby et al. (1991) and Peterson and Black (1988) who found that mid/high intertidal organisms exhibit 2–3 times the expected decrease in growth predicted from submergence time alone.

While significantly greater growth was detected for oysters residing at the surface in the subtidal zone, no significant growth differences between tidal heights were observed below the surface within the reef interstices. The reasons for this are not readily apparent from this study; however, it is likely that any differences in growth rates within the reef interstices were less detectable because differences in submergence time and environmental stress were less pronounced below the reef.

In this study subtidal locations were superior for growth, but oysters residing at the reef surface generally survived best at MLW. This concurs with other studies which have demonstrated that oysters at MLW do not experience the high rates of predation, sedimentation, and fouling that occur at subtidal depths (McDougall, 1942; Chesnut and Fahy, 1953; Marshall, 1954; Nichy and Menzel, 1967), nor do they encounter the severe atmospheric extremes and respiratory stresses associated with higher intertidal levels (Bahr and Lanier, 1981; Potter and Hill, 1982; Michener and Kenny, 1991; Roegner and Mann, 1995).

On average oysters in this study grew most rapidly during the August/September period. Of all the abiotic factors affecting growth in *C. virginica*, Shumway (1996) stated that the synergistic effects of temperature and salinity probably have the most profound influence. Although the optimum range of salinities varies according to geographic range, salinities of about 15–18 ppt represent the physiological optimal ranges (Shumway, 1996). During this study salinities fell within this ideal range during the middle to end of the first sampling period and remained within this range for the rest of the study. Galtsoff (1964) reported highest feeding rates for oysters at water temperatures of 25–26°C, and these temperatures were most often encountered during the August/September period. Thus, both optimal salinities and water temperatures were present during the August/September period, and this may have favored faster growth. An additional factor that may have contributed to high growth during the August/September sampling period was turbidity (silt or seston concentration). Although oysters can feed in water containing relatively large numbers of microorganisms, oysters feed most efficiently in clear, non-turbid waters (Loosanoff and Engle, 1947; Hsiao, 1950). Based on Secchi disk readings, water clarity was greatest during the August/September period, presumably allowing oysters to feed most efficiently. The mechanism(s) responsible for the depression in growth during the July/August periods were not evident from the data in this study.

In this study we had sought to explain variation in oyster growth rates between replicates at a given height based on variance in flow. However, there was a general lack of linear dependence (with the exception of Large oysters at – 90 cm) between growth and dissolution rate, a surrogate measure of flow, which precluded partitioning growth variations according to flow rate. The absence of a consistent relationship between growth and flow probably was not a product of the chlorine tablets. The tablets were reliable predictors of flow when tested in flumes and although sublimation may be problematic when the tablets are exposed to air, dissolution rates recorded at different levels of aerial exposure were never compared.

The relationship between bivalve growth and flow in the field is confounded by the interplay of feeding physiology, seston concentration, and hydrodynamics in the region of the benthic boundary layer (Jorgensen, 1983; Frechette et al., 1989; Vogel, 1994), making it difficult to separate out and assess the effects of flow on growth patterns. Grizzle and Lutz (1989) and Grizzle and Morin (1989) suggested that currents alone were not the best predictors of growth of *Mercenaria mercenaria* in Great Sound, New Jersey because water flow and seston characteristics typically vary widely and concurrently. Instead Grizzle and co-workers suggested that seston fluxes (a product of current speed and seston concentration), especially horizontal fluxes, were more closely correlated with growth; growth and seston flux were positively correlated to a point, after which growth declined with further elevations in seston flux.

Studies performed in more controlled environments, such as in flumes or pipes, also indicate that there is a complex relationship between growth and flow in bivalves. Kirby-Smith (1972) determined that bay scallops *Argopecten irradians* grow faster with decreasing flow rates below 12 cm/s, provided chlorophyll levels do not drop below critical levels. Eckman et al. (1989) reported that growth of *A. irradians*, decreases gradually with increasing velocity between 1.4 and 17.2 cm/s but that the extent of the effects varies dramatically with orientation to flow. Cahalan et al. (1989) were unable to

detect a relationship between water flow and growth for *A. irradians* while Wildish et al. (1987) and Wildish and Saulnier (1993) reported that growth of giant scallops *Placopecten magellanicus* is inhibited at high flow velocities (> 10 cm/s) but is enhanced with increasing flows between 0 and 3 cm/s. Grizzle et al. (1992) found that growth of *C. virginica* decreases with increased current flow when current velocities are between 2 and 8 cm/s. However, in a subsequent study where a narrower range of velocities (0–4 cm/s) was examined, Grizzle et al. (1992) found growth is maximized at 1 cm/s and decreases with flows less than or greater than 1 cm/s. Moreover, Lenihan et al. (1996) determined that growth of *C. virginica* increases with both food concentration and flow over a velocity range from 0 to 7 cm/s and that flux, a product of food concentration and flow, does not have a multiplicative impact on growth. The absence of a consistent relationship between growth and flow for *C. virginica* in this study (i.e. positive/negative linear relationship, hyperbolic trend as determined by Grizzle et al. (1992)) suggests that multiple factors may be affecting growth rates at the reef site.

Oyster reefs have levels of surface and interstitial heterogeneity that may be unmatched in temperate estuaries. This study demonstrates that the principle inhabitant of oyster reefs, oysters, may benefit from this inherently complex environment. Residence merely 10 cm beneath the reef substrate may enhance growth at particular tidal elevations and substantially elevate survival during periods of intense solar exposure and predation. Likewise, variation in tidal elevation may significantly affect oyster growth and survival. Thus, spatial position within a 3-dimensional reef habitat plays a critical role in the biology and ecology of *C. virginica*.

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