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The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*

by C. H. Peterson,¹ H. C. Summerson¹ and P. B. Duncan¹

ABSTRACT

The average density of *Mercenaria mercenaria* in 216 $\frac{1}{4}$ -m² samples taken in spring 1980 from an eelgrass (*Zostera marina*) bed in Back Sound, North Carolina, was 9.0 m⁻², more than five times the average density (1.6 m⁻²) in 216 $\frac{1}{4}$ -m² samples from a nearby sand flat. Size-frequency distributions differed between environments, with the sand flat containing a larger fraction of its *Mercenaria* in the smallest size class (0–1 cm). Use of internal growth lines to age all *Mercenaria* collected revealed that age-frequency distributions also differed between environments but that average *Mercenaria* age was identical in the two collections. The average sizes of 0-, 1-, and 2-year-class *Mercenaria* were significantly greater in the seagrass collection. Furthermore, the logarithmic growth curve fit through the mean sizes of each year class for the seagrass collection fell significantly above the analogous sand-flat curve for all ages, implying higher growth rates inside the seagrass environment.

The seagrass environment contained a higher proportion of finer sediments, more silts and clays, and higher organic content both in surface (0–2 cm) and in deep (0–20 cm) cores. Current velocities measured by dye release in the field demonstrated a substantial baffling effect by the seagrass, with average surface velocities above the blades about 3–5 × average velocities at depths within the seagrass canopy. This baffling by seagrass reduced currents near the bottom, where *Mercenaria* feeds, to levels 50% lower than those measured simultaneously on the sand flat. The paradoxically higher growth rate of the filter-feeding *Mercenaria* in the lower current regime inside the seagrass bed may be a consequence of higher particulate food concentrations produced by the hydrodynamic baffling of the emergent vegetation.

1. Introduction

Marine benthic ecologists have long realized that the presence of emergent macrophytes greatly influences the coexisting benthic fauna. For example, where grazing is reduced on coral reefs, benthic algae can replace live corals (Vine, 1974; Potts, 1977; Birkeland, 1977; Sammarco, 1980). On rocky intertidal shores, attached macrophytes can shelter the epifauna from both desiccation (Dayton, 1971) and predation (Suchanek, 1978), compete effectively with attached epifauna by using the whiplash from their fronds, stipes, and blades in the currents (Lewis, 1964), and offer

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necessary habitat for various associated invertebrates (Choat and Kingett, 1982). Similar direct effects of emergent vegetation have been demonstrated in marine soft substrata. Marsh grasses can reduce the effectiveness of large consumers (Vince *et al.*, 1976; Van Dolah, 1978) and the roots and rhizomes of seagrasses can inhibit digging or burrowing predators (Orth, 1977; Reise, 1977; Virnstein, 1977; Stoner, 1980; Peterson, 1982), while emergent blades interfere with above-ground consumers (Nelson, 1979; Coen *et al.*, 1981; Heck and Thoman, 1981). In these soft-bottom examples, the physical structure of the macrophytes creates partial prey refugia. Macroalgae also influence benthic macrofaunal communities directly by providing specific chemical clues that induce settlement of certain species (Ryland, 1959; Williams, 1964; Meadows and Campbell, 1972; Morse *et al.*, 1979).

In addition to such direct effects, emergent benthic vegetation can have important indirect effects on benthic animals. Salt marsh vegetation (Van Straaten and Kuenen, 1958) and seagrasses (Ginsburg and Lowenstam, 1958; Orth, 1977; Brenchley, 1978) stabilize otherwise mobile sediments, altering the community composition and trophic structure of the benthic fauna (Rhoads and Young, 1970; Rhoads, 1974). The emergent structure of the plants baffles the current flow by deflecting currents around (in the intertidal) or upward and over (in the subtidal) the vegetation. This process (well described for an algal-covered rocky shoreline by Ott (1967), for a seagrass bed by Fonseca *et al.* (1982, 1983), and for a kelp forest by Jackson and Winant (1983)) creates relatively low water flow near the bottom and thus produces enhanced deposition of all materials in suspension, such as fine sediments, invertebrate larvae, plankton, and detritus. Deposition is especially intense at the edge of the macrophyte bed, where the dynamic alteration in velocity profile occurs (Bernstein and Jung, 1979; Bray, 1981; Tegner and Dayton, 1981).

Here, we provide results from extensive sampling of a warm-temperate seagrass bed and a nearby unvegetated sand flat to test whether the population structure (density and size-frequency distribution) of a common suspension-feeding bivalve (*Mercenaria mercenaria*) differs with changing environment. We also utilize a tested procedure to age each clam collected and thereby assess whether individual growth rate in *Mercenaria* changes as a function of seagrass presence. We then relate these biological properties to observed differences in local current regimes and sedimentary parameters.

2. Methods

Our field sampling sites (Fig. 1) were all situated along the southern (barrier island) margin of Back Sound 6–8 km northwest of Cape Lookout, North Carolina (USA). Water temperatures in this area vary greatly with season: monthly means measured in nearby Beaufort ranged from 4–29°C over a 3-year period (Sutherland and Karlson, 1977). Salinities remain high year-round because of relatively low riverine input and extensive tidal exchange with the Atlantic Ocean through Barden's Inlet at Cape

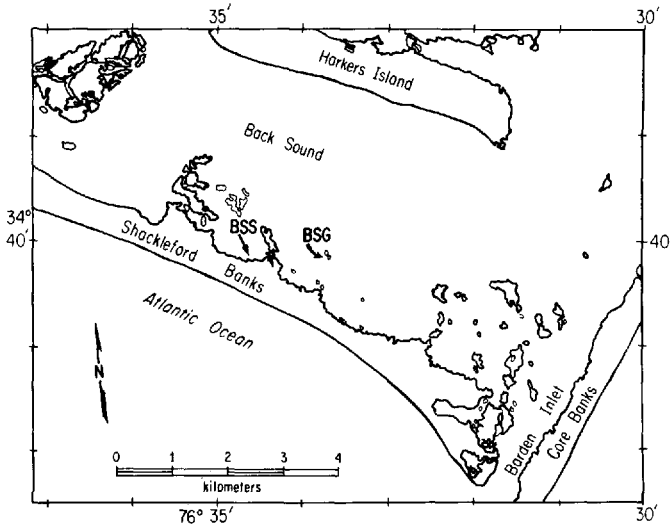


Figure 1. The locations of the study sites in eastern North Carolina, USA, near Cape Lookout. BSS indicates the sand-flat and BSG the seagrass-bed locations. Tick marks on the margins of the figure indicate minutes of latitude and longitude.

Lookout and Beaufort Inlet about 8–10 km west of our sampling sites. In Bogue Sound, which is both physiographically similar to Back Sound and also connected to Back Sound at Beaufort Inlet, daily salinities have remained $>34\text{‰}$ in summer and fall and $>32\text{‰}$ in winter and spring over a decade, except after infrequent (<1 per year) heavy rainstorms, when values of 26‰ have occurred (unpub. data, H. J. Porter, Univ. of North Carolina). Tidal currents in the vicinity of our sampling area reach surface values of only about 10 cm sec^{-1} and wave action is evident only during the north winds of winter.

We selected in January 1980 six replicate 1225-m^2 sampling areas (“matrices”) in a seagrass bed and six in a nearby sand flat about 500 m to the west (Fig. 1). Areas were chosen on the basis of homogeneity of surface appearance: all seagrass matrices contained nearly continuous seagrass cover, whereas macrophytes were virtually absent from all sand-flat matrices. We chose sand-flat matrices as close as possible to the seagrass matrices, constrained by the desire to hold tidal elevation constant across all sampling sites (at 0.2–1.0 m depth at low tide). From aerial photographs taken on 7 April 1974 (National Ocean Survey Project # 74-C(c) in infrared color at a negative scale of 1:60,000) and from our own experience in this vicinity, we knew that all six seagrass matrices had been continuously vegetated from at least 1974 until 1980 and that the seagrass cover had never extended over our sand-flat matrices during that period. To characterize any differences in sediment-size distribution or organic content, we took two sets of three haphazardly located 5-cm diameter sediment cores from each of the 12 matrices: the first set on May 2–3, 1980 to a depth of 20 cm to

describe a broad spectrum of depths and the second on Feb 24, 1983 to a depth of only 2 cm to characterize the surface sediments, which reflect the more recent history of sedimentation. We estimated particle-size distributions by weight using standard Ro-tap sieving and pipetting procedures (Ingram, 1971; Folk, 1974) and organic contents using weight loss by ignition at 550°C for 4 hours (Gross, 1971).

To test whether the presence of seagrasses effectively baffles water currents at our study site, we estimated current velocities for one full tidal cycle on each of two occasions, July 11 and Aug 10, 1983. Three replicate flow measures were made at each of three locations every 20 min over the 12½-hr cycle by releasing from a pipette a drop of concentrated rose bengal dye and timing its passage over a measured track. Measurements were made 18 cm from the bottom on the sand flat and at 18 cm and 35 cm in the seagrass bed (representing points substantially below and just above the relatively fixed, 30 cm-high canopy). All measurements were made at sites of equal elevation (about 0.4 m deep at lowest tide). Water depth was also measured every 20 min at both the seagrass and sand-flat localities while the current velocities were measured. The dates chosen were characterized by light winds (<10 km hr⁻¹) and spring tides (local tidal datum ranging from 0.8 [or 0.9] to -0.1 to 1.0 m), so as best to illustrate relative relationships in current velocities among the three measurement locations without added variance from wind turbulence.

To estimate both seagrass dry weight and the density of *Mercenaria mercenaria* and to gather quantitative samples to permit estimation of age distribution, size distribution, and individual growth rate of *Mercenaria* in both the seagrass and sand-flat environments, we took 36 uniformly distributed ¼-m² samples from each matrix. Sampling in the sand flat was conducted from 22 Feb 1980 – 31 March 1980, whereas the seagrass matrices were sampled from 1 April 1980 – 3 May 1980. To collect a sample, we first isolated each ¼-m² location from the surrounding sediments by inserting a circular metal sampling frame to a depth of 15 cm. We then used a gasoline-powered hydraulic suction dredge to excavate each frame to a depth of 15 cm. The contents were deposited in nylon bags with 3-mm mesh to permit both *Mercenaria* and seagrass material to be sorted from the sediments and other benthos. This process has been demonstrated to be ≈100% efficient and nonsize-selective for all *Mercenaria* >5 mm in length (Peterson *et al.*, 1984). All living *Mercenaria* from each sample were placed into separately marked plastic bags and returned to the laboratory. All seagrass material (both above- and below-ground components) from each sample was bagged separately and returned to the laboratory, where attached sediments were gently rinsed away with distilled water and each sample of seagrass was dried to constant weight at 105°C.

In the laboratory, clams were killed by heating in a drying oven. The number of *Mercenaria* in each sample was counted and recorded. Each clam was also measured to the nearest 0.1 mm along the longest antero-posterior axis (length) using vernier calipers. One valve of each clam was sectioned from the umbo to the ventral margin

Table 1. Average (\pm SD) dry weight of seagrass and density of *Mercenaria mercenaria* per $\frac{1}{4}$ -m² sample in 6 replicate sample matrices (1225 m² each) in both a seagrass bed and a sand flat. 36 $\frac{1}{4}$ -m² samples were taken from each matrix and collected in 3-mm mesh bags.

Sample matrix	Average g dry weight of seagrass per $\frac{1}{4}$ -m ² in:		Average <i>Mercenaria</i> density* per $\frac{1}{4}$ -m ² in:	
	Seagrass bed	Sand flat	Seagrass bed	Sand flat
1	10.4(\pm 14.3)	0.0	2.42(\pm 2.64)	0.36(\pm 0.87)
2	28.4(\pm 25.0)	0.0	2.56(\pm 2.17)	0.50(\pm 0.85)
3	41.2(\pm 24.2)	0.0	1.83(\pm 1.48)	0.47(\pm 0.81)
4	19.6(\pm 15.7)	0.0	2.28(\pm 2.01)	0.25(\pm 0.55)
5	14.4(\pm 13.4)	0.0	2.28(\pm 1.72)	0.33(\pm 0.59)
6	16.0(\pm 20.9)	0.0	2.19(\pm 2.27)	0.47(\pm 0.77)
Average	21.7(\pm 21.9)	0.0	2.26(\pm 2.07)	0.40(\pm 0.75)

*In a nested ANOVA on log ($x+1$)-transformed *Mercenaria* densities, the difference between environments is highly significant ($P < 0.001$), while differences among matrices within either environment are nonsignificant ($P > 0.05$).

along the axis of greatest growth. The shell cross section was then sanded and polished to permit aging by counting annual bands on the cross-sectional surface. This aging process has been shown to be at least 93% accurate over 3 years in a mark-recapture study done in Back Sound, North Carolina (Peterson *et al.*, 1984). From individual lengths and ages, we were able to construct individual growth curves for *Mercenaria* in each environment as a test of whether the presence of abundant seagrass has any influence (direct or indirect) on the individual growth rate of a common suspension-feeding bivalve.

3. Results

Our collections of all above- and below-ground seagrass material from the 36 $\frac{1}{4}$ -m² samples in each matrix (Table 1) revealed that all six replicate seagrass matrices were indeed characterized by abundant seagrass, whereas no macroscopic seagrass material was collected from any of the six replicate sand-flat matrices. The mean dry weight of seagrass per $\frac{1}{4}$ -m² ranged from a low of 10.4 g \pm 14.3 (SD) in seagrass matrix 1 to a high of 41.2 g \pm 24.2 (SD) in seagrass matrix 3 (Table 1). The average dry weight of seagrass over all six seagrass matrices was 21.7 g \pm 21.9 (SD) per $\frac{1}{4}$ -m². During our Feb–May 1980 sampling period, the seagrass bed was dominated by eelgrass (*Zostera marina*): about 80% of all seagrass shoots was eelgrass, while the remaining 20% was shoalgrass (*Halodule wrightii*).

A 2-way, nested, mixed-model ANOVA demonstrated that *Mercenaria* density did not differ significantly ($\alpha = 0.05$) among the six replicate sample matrices within either the sand flat or the seagrass bed (Table 1). However, average *Mercenaria* density inside the seagrass matrices was more than five times the average sand-flat

density ($P < 0.001$). The analysis was performed on $\log(x+1)$ -transformed densities because this transformation was sufficient to homogenize variances within each habitat (using two separate Bartlett's tests) and between habitats (using an F-test comparing variances among matrix means). Despite the large between-matrix range in average seagrass dry weights (10.4–41.2 g per $\frac{1}{4}$ m²), there was no significant correlation between average *Mercenaria* density and average seagrass dry weight among the seagrass matrices (Table 1). Furthermore, the number of *Mercenaria* in each individual sample from the seagrass environment was not significantly related to the seagrass dry weight in that sample, using all samples from the six seagrass matrices.

Analysis of sediment-size distributions and of organic content demonstrated little difference within either environment between replicate matrices or between deep cores taken to 20 cm and surface cores taken to a 2-cm depth (Table 2). The only significant difference between deep and shallow particle-size distributions appeared in the seagrass environment (Table 2), where the deeper sediments were somewhat more poorly sorted than the shallow ($P < 0.01$ in a 2-way, nested ANOVA on the inclusive graphic standard deviation). Even this difference was not large. However, the sediment-size distributions differed greatly between the two environments. Smaller particles contributed much more to the seagrass sediments. For instance, on average over all six replicate matrices, silts and clays together comprised from 13.6 (shallow) to 18.2 (deep) percent by weight of all seagrass sediments compared to from 2.6 (shallow) to 2.2 (deep) percent on the sand flat. Consequently, graphic mean ϕ values were significantly ($P < 0.001$ in nested ANOVA's) greater in the seagrass environment. Furthermore, the seagrass sediments were significantly more poorly sorted, the seagrass sediment-size distributions were fine-skewed rather than symmetrical as in the sand flat, and they were very leptokurtic (Table 2). Organic content was low in both environments, but the average percent organic matter in the seagrass samples was nearly three times ($P < 0.001$) that found in sand-flat sediments (Table 2).

Current velocity measurements (data for the August observation date given in Fig. 2) illustrate the baffling effect of the seagrass bed. The average current velocities above the seagrass canopy (4.2 cm sec⁻¹ on July 9 and 3.7 cm sec⁻¹ on August 10) were 3.2 \times (July) and 5.0 \times (August) the observed average current velocities underneath the canopy. The average difference in current velocities between the location above the canopy and that below was 2.9 cm sec⁻¹ on both dates (significantly different from zero on both dates at $P < 0.001$ in paired t-tests). The average current velocities within the seagrass canopy were 41% (July) and 55% (August) lower than the average current velocities at the same 18 cm level in the water column over the sand flat. The average difference in current velocities between the sand flat and the below-canopy location in the seagrass bed was 0.9 cm sec⁻¹ on both sampling dates (significantly different from zero on both dates at $P < 0.001$ in paired t-tests). Water levels measured every 20 min over the full tidal cycle (Fig. 2) agreed with the current velocity measurements in

Table 2. Average percent dry weights of sediments in each of several particle-size classes from shallow (0-2 cm) and deep (0-20 cm) cores taken in each seagrass and sand-flat matrix. Averages are from 3 sediment cores of each penetration depth in each matrix. Percentages do not sum to 100 because larger size classes are not included. Lower portion of table represents average parameters from sediment-size distributions.

Sample location	% dry weight											
	Seagrass environment					Sand-flat environment						
	medium sands	fine sands	very fine sands	silts and clays	medium sands	fine sands	very fine sands	silts and clays	medium sands	fine sands	very fine sands	silts and clays
Matrix 1—shallow	12.4	63.2	16.0	5.9	37.1	58.2	1.6	1.2	37.1	58.2	1.6	1.2
Matrix 1—deep	16.6	53.0	8.0	14.1	37.4	57.8	1.6	1.5	37.4	57.8	1.6	1.5
Matrix 2—shallow	7.5	58.1	21.8	9.7	32.8	60.6	2.5	2.6	32.8	60.6	2.5	2.6
Matrix 2—deep	16.0	57.4	11.2	12.3	33.9	59.2	2.5	2.0	33.9	59.2	2.5	2.0
Matrix 3—shallow	6.6	58.3	23.5	10.0	23.5	65.9	5.1	3.6	23.5	65.9	5.1	3.6
Matrix 3—deep	13.5	51.3	12.9	19.6	33.0	59.5	3.1	2.1	33.0	59.5	3.1	2.1
Matrix 4—shallow	5.3	52.2	26.2	14.4	34.1	59.2	3.1	2.2	34.1	59.2	3.1	2.2
Matrix 4—deep	10.1	44.9	20.0	23.2	36.4	56.1	2.4	2.7	36.4	56.1	2.4	2.7
Matrix 5—shallow	8.9	48.8	24.1	17.0	16.8	74.2	5.3	2.9	16.8	74.2	5.3	2.9
Matrix 5—deep	12.7	48.7	13.9	22.6	31.6	60.4	2.4	2.8	31.6	60.4	2.4	2.8
Matrix 6—shallow	11.1	40.1	22.4	24.3	27.7	62.4	3.7	3.3	27.7	62.4	3.7	3.3
Matrix 6—deep	21.8	43.4	14.5	17.4	30.7	62.7	2.5	2.0	30.7	62.7	2.5	2.0
Average—shallow	8.6	53.4	22.3	13.6	28.7	63.4	3.6	2.6	28.7	63.4	3.6	2.6
Average—deep	15.1	49.8	13.4	18.2	33.8	59.3	2.4	2.2	33.8	59.3	2.4	2.2

Average parameter value*

Sediment size-distribution parameter	Seagrass environment			Sand-flat environment		
	Shallow cores	Deep cores	Average parameter value*	Shallow cores	Deep cores	Average parameter value*
Graphic mean (M_z)	2.98	3.00		2.24	2.15	
Inclusive graphic standard deviation (σ_I)	1.14	1.66		0.58	0.53	
Inclusive graphic skewness (SK_I)	0.35	0.41		0.04	-0.05	
Graphic kurtosis (K_G)	1.82	2.18		1.31	1.11	
% organic content	1.76	1.67		0.63	0.66	

* All differences between seagrass and corresponding sand-flat parameters were statistically significant at $P < 0.001$ (except graphic kurtosis for shallow cores at $P < 0.01$) in nested ANOVA's performed on data transformed, as follows, to homogenize variances: $(\log M_z, \log \sigma_I, \arcsin \sqrt{(1 + SK_I)/2}, K_G/(1 + K_G), \text{ and } \arcsin \sqrt{(\% \text{ organic}/100)})$.

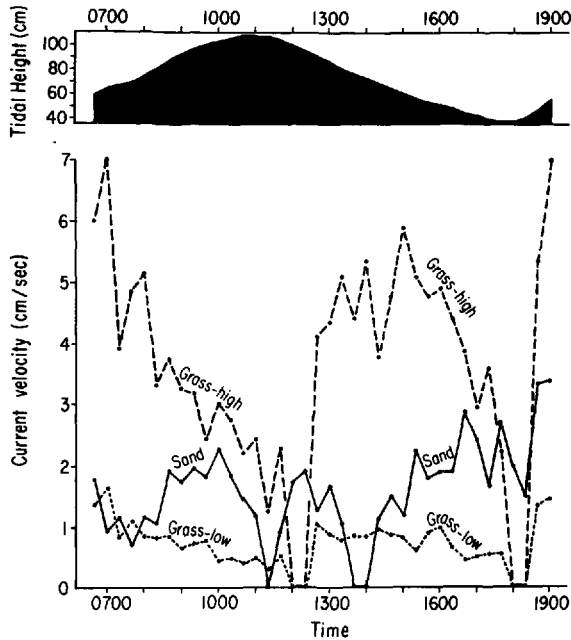


Figure 2. Tidal current velocities over a full ($\approx 12\frac{1}{2}$ hr) tidal cycle at two depths (18 and 35 cm above the bottom) in a seagrass bed and at one depth (18 cm) on a sand flat. Measured tidal elevations on the sand flat (the seagrass pattern was identical) are plotted above. The seagrass canopy projected upward to a level of about 30 cm above the bottom. Each point in the current velocity plots represents the average of three replicate current measures made in the direction of flow by observing dye release on a spring tide (August 10, 1983). Solid lines connect sand-flat data, short dashes (grass-low) connect the 18 cm data in the seagrass bed, while long dashes (grass-high) connect the 35 cm data in the seagrass bed. Paired t-tests show average current velocities to differ significantly between the two depths in seagrass ($t_{37 \text{ d.f.}} = 12.20$; $P < 0.001$) and between the two environments at 18 cm depth ($t_{37 \text{ d.f.}} = 6.31$; $P < 0.001$).

showing the asymmetry of tidal flux: flood tides produce stronger currents but over shorter times than ebb tides. Curiously, slack tides seemed to occur somewhat after the absolute maximum and absolute minimum in tidal height were reached (Fig. 2).

For each environment, we pooled clam data from all 216 $\frac{1}{4}$ -m² samples to estimate the two size (length)-frequency distributions of *Mercenaria* (Fig. 3). These size-frequency distributions include all 488 *Mercenaria* collected in the seagrass and 85 of the 86 individuals collected from the sand flat (one clam was crushed by insertion of the sampling frame). A χ^2 test revealed that the two size-frequency distributions differ significantly ($P < 0.001$). Inspection of the two distributions (Fig. 3) demonstrates that the smaller clams (0–1 and 1–2 cm in length) were proportionately more abundant in the sand flat, while larger individuals (all six size classes >4 cm in length) were proportionately more common in the seagrass bed.

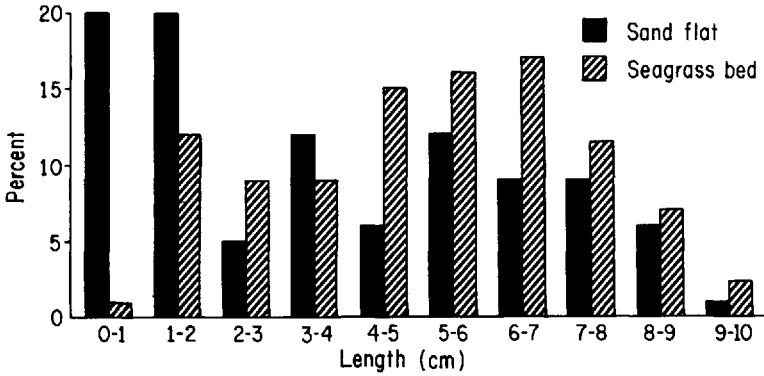


Figure 3. The size (length)-frequency distributions of (1) all 488 *Mercenaria mercenaria* collected from 216 $\frac{1}{4}$ -m² samples taken in seagrass and (2) 85 of the 86 (1 lost to breakage) *Mercenaria* collected from 216 $\frac{1}{4}$ -m² samples taken in the sand flat. The two distributions differ significantly ($\chi^2_{(9 \text{ d.f.})} = 78.3$; $P < 0.001$).

Age-frequency distributions (Fig. 4), constructed by pooling all 488 clams collected from the seagrass and again 85 of the 86 individuals gathered from the sand flat, provide a partial explanation for the differing size-frequency distributions. The age-frequency distributions of *Mercenaria* differed significantly between the two environments ($P < 0.001$ in a χ^2 test). Figure 4 shows that the largest difference in age structure between environments occurred in the 0-year class, which contains 40% of all individuals collected from the sand flat but only 22% of all seagrass *Mercenaria*. No other difference was so large and average age class did not differ significantly (at $\alpha = 0.05$ in a t-test) between environments (2.96 in the sand flat vs. 2.88 in the seagrass

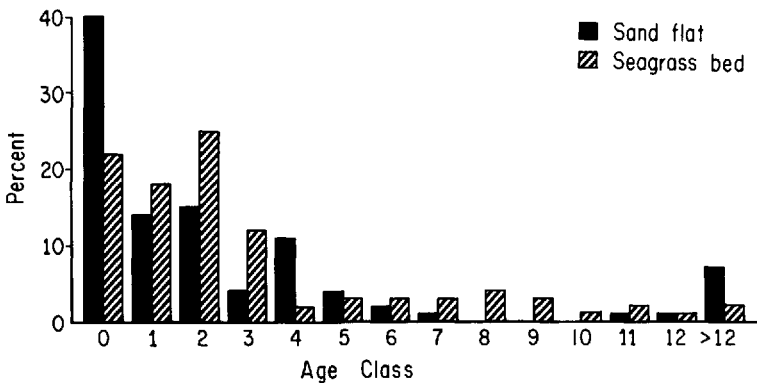


Figure 4. The age-frequency distributions of (1) all 488 *Mercenaria mercenaria* collected from 216 $\frac{1}{4}$ -m² samples taken in seagrass and (2) 85 of the 86 (1 lost to breakage) *Mercenaria* collected from 216 $\frac{1}{4}$ -m² samples taken in the sand flat. The two distributions differ significantly ($\chi^2_{(10 \text{ d.f.})} = 46.7$; $P < 0.001$ — all age classes >9 are combined in this analysis).

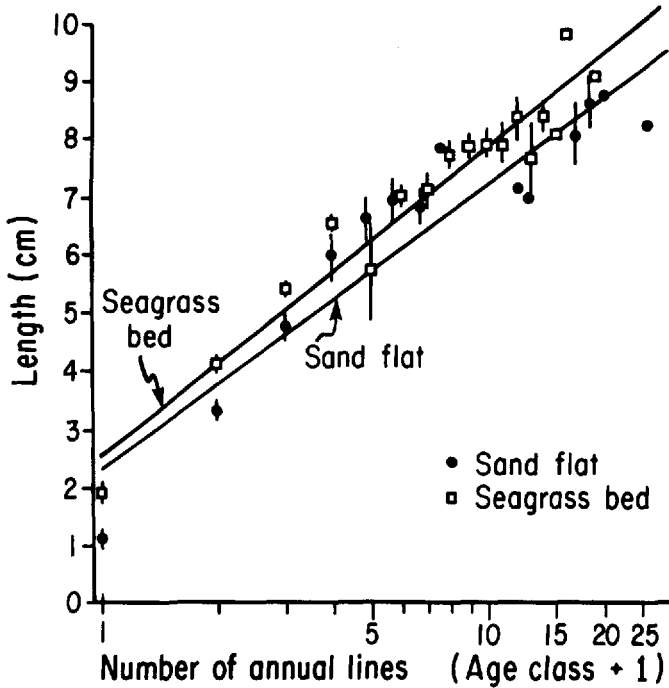


Figure 5. The average (± 1 SE indicated with bars) size of all sand-flat and all seagrass *Mercenaria mercenaria* in each year class. Sample sizes can be calculated for each age class and habitat by using the age-frequency information given in Figure 4 and average densities given in Table 1. Sampling was done from 22 Feb–31 March 1980 in the sand flat and from 1 April–3 May 1980 in the seagrass bed. Assuming an average recruitment date of about mid July, estimated age (in years) of sand-flat clams is calculated by age class + $\frac{3}{4}$ and of grass-bed clams by age class + $\frac{3}{4}$. Some seagrass points were displaced slightly to the right to avoid overlap of error bars. Statistically significant differences between habitats in size appear in age class 0 ($t_{(140 \text{ d.f.})} = 4.53$; $P < 0.001$), age class 1 ($t_{(96 \text{ d.f.})} = 3.19$; $P < 0.001$), and age class 2 ($t_{(132 \text{ d.f.})} = 2.64$; $P < 0.01$). ANCOVA shows a significant ($P < 0.05$) difference between the two logarithmic growth curves (as drawn on the graph): in the seagrass, $y = 2.54 + 2.28 \ln x$, where y is clam length in cm and x is number of annual lines (age class + 1) ($r^2 = 0.93$; $P < 0.001$) and, in the sand flat, $y = 2.33 + 2.10 \ln x$ ($r^2 = 0.88$; $P < 0.001$).

bed). In both environments, approximately 75% of all individuals was less than or equal to the mean age class of 3 (Fig. 4).

We utilized our age estimates together with *Mercenaria* length measurements to construct two plots of how average clam size changes with age class: one for all clams collected from the sand flat and the other for all seagrass clams (Fig. 5). Two-tailed t-tests, performed to compare the average sizes of each age class between environments, revealed that average *Mercenaria* sizes were greater in the seagrass collection in the 0-year class ($P < 0.001$), the 1-year class ($P < 0.001$), and the 2-year class ($P < 0.01$). Although no other year class revealed a significant size difference between

environments, the lack of significance in older year classes appears to be largely a consequence of lower sample sizes. Logarithmic growth curves fit through the mean sizes of each age class (Fig. 5) reveal a statistically significant separation between the two curves ($P < 0.05$ in ANCOVA evaluated at the grand mean of the year classes represented, 8.6). T-tests reveal that slopes of the two curves do not differ significantly ($P > 0.50$), implying that ANCOVA is an appropriate analysis. ANCOVA evaluated at year-class 30 (31 annual lines) shows that the mean expected size of seagrass *Mercenaria* (10.4 cm) is still significantly greater than that of sand-flat individuals (9.5 cm). All of these same conclusions hold when the ANCOVA is carried out on data from just those (older) age classes (from age class 3 on) which do not show significant size differences between environments in the t-tests. Similarly, ANCOVA run on individual data points, rather than on mean sizes of each age class, reveals parallelism of the two logarithmic growth curves and significant differences in growth between the two environments ($P < 0.001$ using all data points and $P < 0.05$ using age-classes 3 and above).

4. Discussion

Because many previous studies have demonstrated higher infaunal densities in temperate-zone seagrass beds than in surrounding unvegetated sediments (e.g., O'Gower and Wacasey, 1967; Santos and Simon, 1974; Orth, 1977; Brook, 1978; Stoner, 1980), we were not surprised to find *Mercenaria* to be significantly more abundant in our seagrass-bed samples (Table 1). Furthermore, Peterson (1982) had shown significantly higher *Mercenaria* densities in a *H. wrightii* meadow in nearby Bogue Sound, North Carolina, than in an adjacent sand flat. The density data presented here (Table 1) merely extend that result to a seagrass system dominated by eelgrass (*Z. marina*) instead of shoalgrass (*H. wrightii*). The lack of a significant relationship between seagrass dry weight and *Mercenaria* abundance among seagrass matrices or among $\frac{1}{4}$ -m² samples within the seagrass environment implies that the effect of seagrass on *Mercenaria* abundance operates on a large, rather than a local, scale and that the seagrass influence is achieved at a level of 10 g per $\frac{1}{4}$ m² and does not increase with further increases in seagrass cover.

The lack of difference between environments in the average age of *Mercenaria* and the generally small differences in age distributions (Fig. 4) are surprising. If whelks (predatory gastropods of the genus *Busycon*) are a major cause of mortality among large *Mercenaria* in unvegetated sand flats in North Carolina but are relatively ineffective within seagrass beds (as demonstrated by experimental results in Peterson, 1982), then one would expect seagrass beds to accumulate older clams. Yet the age-frequency distributions (Fig. 4) show no such pattern of enhanced dominance by older age classes in the seagrass collection. There is, however, a suggestion in the age-frequency data (Fig. 4) that differential rates of human predation on seagrass-bed

Mercenaria may be an important explanation of this paradoxical identity in average clam age.

Clamming is a major fishery in this region of North Carolina (Peterson *et al.*, 1984). *Mercenaria* cannot be legally harvested in North Carolina until it reaches a 2.54 cm thickness, corresponding to a length of ≈ 4.5 cm (Peterson *et al.*, 1984). Figure 5 suggests that this size is usually achieved sometime between a clam's second and third winter seasons in both seagrass and sand-flat environments at our study site. Consequently, human predation would only begin to be experienced by clams in age class 2 and should be most effective in reducing abundances of subsequent age classes. By converting the percentages in Figure 4 to absolute numbers in each age class, a pattern emerges that is at least consistent with the suggestion of differential rates of human predation. In the 0-year class, *Mercenaria* density in the seagrass was only 3.2 times (108/34) the sand-flat density. Yet, averaged over the next 3 year classes, which represent sizes (Fig. 5) that whelks take readily (Peterson, 1982) but that human clamming can only begin to affect, the density of *Mercenaria* in seagrass was 9.4 times (264/28) the sand-flat density. In all older (>3) age classes, *Mercenaria* density was only 5.0 times (116/23) higher in the seagrass collection. Assuming that these age distributions in Figure 4 faithfully reflect between-habitat differences in survivorship, they suggest that sand-flat clams suffer higher early (from the 1st to the 2nd winter) mortality than seagrass clams, but that mortality rates after the 3rd or 4th winter are higher for seagrass clams. It is conceivable that clambers recognize the density difference between environments (Table 1) and concentrate most of their shallow-water fishing efforts in the more densely populated seagrass beds. This suggestion of differential rates of human predation between environments could explain the failure of the Back Sound seagrass bed to accumulate relatively old *Mercenaria*.

The most interesting, and surprising, result of this study is the apparent difference in *Mercenaria* growth rates between environments (illustrated in Fig. 5). Unlike the age-distribution data, this difference is not confounded by any effects of human interference. The 0-, 1-, and 2-year-class *Mercenaria* were significantly larger in the seagrass environment and the logarithmic growth curves over all year classes and over older (3 and above) year classes also differed significantly between environments. Although the seagrass bed was sampled approximately 1 month after the sand flat, this difference is insufficient to account for the large size differences between habitats. It is conceivable, although highly unlikely, that a between-habitat difference in the size selectivity of predation (or some other mortality factor) could explain this result. It is even possible that larval recruitment could have occurred earlier in the season in the seagrass environment. However, the most likely explanation of these size differences within year classes is that growth rate was more rapid in the seagrass environment.

As a general axiom, filter-feeding bivalves, including *Mercenaria mercenaria*, are thought to grow faster wherever water currents are greater (e.g., Kerswill, 1949; Pratt and Campbell, 1956). Kerswill (1949) even showed by experimental introduction and

recapture of marked *Mercenaria* that growth rates were lower in a Nova Scotian seagrass bed than in an adjacent unvegetated bottom. Presumably because of baffling by the seagrass blades, current velocities were significantly lower in the Nova Scotian seagrass environment. We observed generally lower current velocities at 18 cm above the bottom inside a seagrass bed than on nearby sand flats (Fig. 2). Measurements of the currents both above and below the seagrass blade canopy demonstrated clearly the hydrodynamic baffling and redirection of water currents by the projecting plants. Although we measured current velocities on only two replicate tidal cycles, the substantially finer character of the surface sediments in the seagrass bed (Table 2) implies a generally lower-energy environment (e.g., Ginsburg and Lowenstam, 1958; Van Straaten and Kuenen, 1958) and suggests that our observed current differences between environments were not atypical. Despite the similarity in the between-habitat differences in current regimes, our *Mercenaria* growth data (Fig. 5) reveal a pattern exactly opposite to that shown by Kerswill (1949).

This paradox can be explained by examination of the literature on the physiology of feeding in filter-feeding bivalves. In laboratory experiments, more carefully controlled than is possible under field conditions, Walne (1972) showed that the rate of capture of suspended food particles by *Mercenaria mercenaria* and four other filter-feeding bivalves increases not only with increasing current flows but also with increasing food concentrations. The baffling effects of seagrass and other macrophytes projecting into a water column not only slow the current velocities near the bottom but also cause deposition at the dynamic edge of the vegetation patch, where velocities actively decelerate (e.g., Ginsburg and Lowenstam, 1958; Scoffin, 1970; Tegner and Dayton, 1981; Jackson and Winant, 1983; Fonseca *et al.*, 1983). This deposition of suspended materials has the potential to increase concentrations of suspended foods near the bottom where *Mercenaria* feeds. Consequently, accurate prediction of the indirect influence of macrophytes on growth of *Mercenaria* and other filter feeders is complicated by opposing effects of hydrodynamic baffling: reduced growth with the reduction of bottom currents and enhanced growth with the increase in bottom food concentrations. The net direction of the effect is likely to be controlled by the relative strength of the two opposing influences. Literature on the hydrodynamics of baffling suggests that the direction of effect will vary with ambient current velocity, the effectiveness of the baffle (e.g., seagrass blade density), and the distance from the edge of the baffle (Fonseca *et al.*, 1982, 1983). Recently, Beal (1983) confirmed the variable nature of this influence of seagrasses on *Mercenaria mercenaria* growth: in parallel experiments in each of three North Carolina sounds, *Mercenaria* in seagrass grew faster than in unvegetated bottom in one locality, slower in a second locality, and at the same rate in a third site.

Clearly, seagrass beds and sand flats differ in several other characteristics, many of which could affect the growth of *Mercenaria* and other filter feeders. The sediment mobility and geochemistry, for example, differ in ways that could create variable

stresses on *Mercenaria* that may be reflected in variations in growth rate. We propose our hydrodynamic hypothesis, with its implicit conflict between the influences of current reduction and particle deposition, to replace the axiom that higher current velocities uniformly imply higher growth rates in *Mercenaria mercenaria* and other filter feeders. This hydrodynamic hypothesis has support in the molluscan physiology literature (Walne, 1972) and has the potential to explain otherwise contradictory data sets. This hypothesis can be, and must be, further tested, but our explanation of the anomalous pattern of higher growth rates of a suspension feeder inside a seagrass bed than in nearby unvegetated sediments is consistent with an evolving appreciation (Ott, 1967; Bernstein and Jung, 1979; Hulberg and Oliver, 1980; Bray, 1981; Tegner and Dayton, 1981) of the biological importance of indirect effects of emergent structural elements, such as macrophytes, on local hydrodynamics and coexisting biota.

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