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Clam Predation by Whelks (*Busycon* spp.): Experimental Tests of the Importance of Prey Size, Prey Density, and Seagrass Cover

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Abstract

In 57 1-m^2 samples within a meadow of *Halodule wrightii* in Bogue Sound, North Carolina, USA, densities of the clams *Mercenaria mercenaria* and *Chione cancellata* were positively associated with seagrass cover. Where seagrass was experimentally removed, marked individuals of both clam species exhibited high rates of mortality in fine sand sediments during two successive experiments spanning 13 months. In the unaltered (control) seagrass meadow, *M. mercenaria* density remained constant over 13 months and *C. cancellata* density declined at a slower rate than in the unvegetated plots. Seagrass provides these clams with a refuge from whelk (*Busycon carica, B. contrarium*, and *B. canaliculatum*) predation, the major cause of mortality and population decline in experimentally unvegetated plots. In 2 factorial field experiments in unvegetated substratum in which densities of *M. mercenaria* and *C. cancellata* were varied independently, first over 5 levels (0 X, ½ X, 1 X, 2 X, 4 X) and subsequently over 4 levels (0 X, ¼ X, 1 X, 4 X), there was no repeatable intra- or interspecific effect of density on percent survival, or on the rate of any mortality type. Whelk predation fell preferentially on larger size classes of both species, whereas factors which contribute to clam disappearance usually acted more intensely on smaller sizes. Experimental exclusion of large predators by caging demonstrated that even in unvegetated substratum survivorship of both clam species was high in the absence of whelks and other predators. Individuals of *C. cancellata* live closer to the sediment surface than those of *M. mercenaria*, which may explain why seagrass does not serve as effectively to protect them from whelk predation. The mechanism of whelk inhibition may depend upon sediment binding by the *H. wrightii* root mat, which produces a demonstrable decrease in the physical penetrability of surface sediments.

Introduction

An understanding of how predators react to variations in habitat and prey characteristics is often the key to explaining local and, occasionally, biogeographic patterns of animal distribution and abundance observed in nature. Homogeneous prey populations in comparatively simple laboratory environments usually go extinct when enclosed with their predators: some form of complexity in habitat or in the prey population is ordinarily necessary for persistence of both predator and prey (Gause, 1934; Huffaker, 1958). Experiments in marine benthic environments have demonstrated that habitat complexity sufficient to provide prey refuges can be created by worm tubes projecting from the sediments (Woodin, 1978), crevices in intertidal rocks (Menge and Lubchenco, 1981), and even relatively large plants and animals attached to hard substrata (Suchanek, 1978; Russ, 1980). Prey characteristics which successfully inhibit the efficiency of bottom-feeding predators include an ability to occupy a harsh physical environment outside the tolerance range of the predators (e.g. Connell, 1971; Dayton, 1971; Paine, 1974; Menge, 1976; Peterson, 1979a) and an ability to reach sizes large enough to escape the predators' handling capacities (Connell, 1970; Dayton, 1971).

Seagrass in marine soft sediments may provide sufficient structural complexity to inhibit the efficiency of benthic predators and to protect coexisting benthic animals. This mechanism has been hypothesized (Orth, 1977; Virnstein, 1977; Reise, 1977; Peterson, 1979b; Stoner, 1980) to explain the consistently high macrofaunal densities in seagrass beds, as compared to nearby unvegetated substrata. A goal of this paper is to provide an experimental test of this hypothesis, using whelks as predators and two species of shallow-burrowing clams as prey. I include additional field experiments to test whether predation rates by whelks are dependent upon local prey density or upon prey size. An escape either in large size (Connell, 1970) or in local rarity (Luckinbill, 1973) might pro-

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vide a potential mechanism for prey persistence in this system.

Materials and Methods

Study Site and Experimental Species

Experiments were conducted in a shallow, subtidal portion of a shoal-grass bed (*Halodule wrightii*) along the southern (barrier island) shoreline of Bogue Sound, North Carolina, USA. Relatively little riverine input and substantial tidal exchange, predominantly through Beaufort Inlet, maintain year-round high salinities of > 34‰S in summer and fall and > 32‰ S in winter and spring in Bogue Sound except during occasional heavy rainstorms, when values of 26‰ S can occur (unpublished data, H. J. Porter, Univ. of North Carolina). Water temperature in this vicinity varies seasonally with monthly means ranging from about 4° to 29 °C (Sutherland and Karlson, 1977). The study site, 13 km west of Beaufort Inlet, has tidal currents of up to 0.5 m s^{-1} near the water's surface and receives substantial wave action during the six colder months when northerly winds prevail (Au, 1974). Sediments at the study site were predominantly fine sands with < 3% silt-clay by weight.

Two species of relatively large, thick-shelled, shallow-burrowing, suspension-feeding, bivalve molluscs are common in this area: the hard clam *Mercenaria mercenaria* and dog clam *Chione cancellata*. I chose these species as experimental organisms because they can be sampled and replaced without harm to the organism, measured accurately, and marked individually by external etching or painting. Cause of death of a clam can often be accurately inferred from the type of damage done to the clam shell, if recovered. Known predators on *M. mercenaria* and *C. cancellata*, including especially three whelks (*Busycon carica, B. contrarium, B. canaliculatum*) (Magalhaes, 1948; Paine, 1962, 1963) and two crabs (*Menippe mercenaria* and *Callinectes sapidus*) (Carriker, 1951, 1959; Vermeij, 1978), are common in Bogue Sound.

Initial Biological Sampling and Physical Parameters

In preparation for the density manipulation and predator exclusion experiments, in Sept-Oct 1977 I marked off a matrix of 57, approximately evenly spaced, 1-m^2 plots at a low tide depth of 0.2–0.4 m within the large (~20 × 110 m), somewhat patchy *Halodule wrightii* bed. Approximately 2-m spaces were left between rows and columns of plots to provide access for sampling. To delineate these plots from the surrounding sediments and to restrict emigration of clams in the experiments to follow, I installed mesh enclosures around each plot. Enclosures consisted of 15-cm-high strips of 6-mm plastic mesh (Dupont VEXAR), attached by nylon cable ties to 1.5-m metal rebar rods at each corner and at half-way points along each enclosure wall. Enclosure walls and anchoring rebar stakes were forced into the sediments such that each wall extended to an 8–10 cm depth below the sediment surface.

After installation of all enclosures, each enclosed plot was characterized visually as (1) unvegetated, (2) partially or thinly vegetated, or (3) thickly vegetated. Then all above- and below-ground seagrass material, clams, and other large macrofauna were removed by using fingers to plow the sediments systematically to a depth of 10 cm and by subsequent, systematic *in situ* sieving through 6-mm mesh to a 10-cm depth. The 6-mm mesh size corresponded to the mesh size of the enclosure walls such that all marked clams used in the experiments would be retained effectively within the enclosures. A second sieving in Oct 1977 of ten 1-m^2 plots through 1-mm mesh increased the total counts of *Mercenaria mercenaria* and *Chione cancellata* by less than 4% (3 < 6 mm *vs* 87 > 6 mm, and 2 < 6 mm *vs* 71 > 6 mm, respectively), implying that at least in that season a 6-mm mesh provided a nearly complete population estimate. All clams encountered were counted by species and measured along the antero-posterior axis to yield length estimates. This initial sampling was sufficient to construct initial size frequency distributions for *M. mercenaria* and *C. cancellata* and to test whether abundance of either species was related to degree of grass cover within the bed of *Halodule wrightii*. To test the accuracy of the visual estimation of seagrass cover within plots, the wet weight of all seagrass removed (broken down into above- and below-ground components by clipping roots and rhizomes from blades and shoots) was measured for the first 4 plots in each of the 3 seagrass cover categories.

In April 1981, the study site was revisited to collect data on variation of the physical environment with the presence and absence of seagrass. Three 4.8-cm diameter sediment cores were taken to a depth of 10 cm at positions within the dense vegetation and in adjacent unvegetated patches. Standard grain size analysis (Folk, 1974) was performed on each core. In addition, I designed and employed a "penetrometer" (analogous to the rotational viscometer used by Meyers, 1977) to estimate the relative ease of penetrating sediments with and without seagrasses. The penetrometer consisted of a 1.417-kg cylindrical rod with a cross-sectional surface of 8.0 cm^2, maintained in a vertical position by loose-fitting brackets on a wooden support. The rod was carefully positioned at the sediment surface and then released. Calibrated marks on the wooden support were used to measure the penetration depth of the rod over a 3-min period. After 3 min, a 454-g weight was dropped a fixed distance in air of 1.25 m to provide taps of repeatable force to drive the rod further into the sediments. I recorded the number of taps necessary to penetrate the top 10 cm. Six replicate readings were taken in both the dense seagrass and in the unvegetated sand patches. In each case, the rod was positioned to avoid beginning on the top of above-ground vegetation or shell debris.

Density Manipulations

To test the possible effects of varying intra- and interspecific clam density on survivorship and type and rates of mortality, I returned *Mercenaria mercenaria* and *Chione cancellata* to the field enclosures at varying densities in a factorial design. I used all combination pairs of the following density treatments: 0 X, ½ X, 1 X, 2 X, and 4 X, where X represents the initial control density (7 m^{-2}) for each species. Each density treatment was assigned at random to one of the 57 positions, with the complete design requiring 25 enclosures. For each species, I utilized the naturally occurring, broad size distribution, which I held constant over all density treatments. Each individual clam was measured and marked uniquely on both valves with color-coded dots of Mark-Tex Corp. paint prior to its return to an enclosure. This experiment continued from Oct 1977 until May 1978, when the initial sampling process was repeated in each enclosure. Empty clam valves and living clams were collected, identified to individual (if marked), and measured.

In July 1978, I established within the same matrix of enclosures a second set of varying densities of *Mercenaria mercenaria* and *Chione cancellata* to test whether survivorship and type and rates of mortality were dependent upon intra- or interspecific density during the warmer months. Densities were varied in a factorial design over 4 levels: 0 X, ¼ X, 1 X, and 4 X, where X again equalled 7 m^{-2} for each species. Each density treatment was assigned at random to one of the 57 enclosures, with the complete design requiring 16 enclosures. Clams used in this second experiment included marked survivors from the first density manipulation experiment, distributed in equal proportion among all treatments, and additional clams collected in the vicinity of the experimental area. Size frequencies were held constant over all density treatments. Painting, measuring, and enclosing procedures were identical to those of the initial experiment. Final sampling, measuring, and data recording occurred after 4 months in Nov 1978.

Interpreting Clam Mortality and Loss

Upon resampling these open enclosures, all initially marked clams were found to be either (1) alive, (2) missing, (3) dead as empty, undamaged shells, (4) dead with shells rasped on the ventral margin, or (5) dead with shells crushed or chipped in multiple positions along the ventral margin. Occasionally, an entire valve was fractured in a Category 4 shell.

Category 4 shell damage is attributable to whelk predation (Magalhaes, 1948; Carriker, 1951; Paine, 1962). To confirm this inference and to test for differences among the three common whelk species, I placed 25 clams of both prey species in complete size ranges in each of 4 aquaria in a running seawater system. Sediments were fine sands collected from Bogue Sound and added to a depth of 5 cm. I introduced 3 individual whelks into each of 3 aquaria, maintaining each species separately, and left the fourth aquarium as a control. Over 10 months, dead clams were collected at approximately 5-wk intervals and replaced by living clams of the same species and size. On no occasion was there as much as 50% mortality in either species of prey.

In the control tank, the only mortality was a pair of deaths of *Chione cancellata,* leaving undamaged shells. Clam mortality that occurred in the tanks with *Busycon carica* and *B. contrarium* was similar: 35 *Mercenaria mercenaria* and 25 *C. cancellata* died in the tank with *B. carica,* while 32 *M. mercenaria* and 19 *C. cancellata* died in the tank with *B. contrarium.* All mortality except that of 1 *C. cancellata* in the tank with *B. carica* and 1 *M. mercenaria* in the tank with *B. contrarium* was of the type categorized as type 4 in the field. I could not distinguish between these two whelks on the basis of either degree or characteristics of damage done to the shells of consumed clams.

Mortality in the tank with *Busycon canaliculatum* totalled only 3 *Mercenaria mercenaria* and 15 *Chione cancellata.* Shell damage, although categorized as Type 4 in every case, was more subtle than that caused by the other two species, as might be predicted from the much thinner shell of *B. canaliculatum* (Paine, 1962). Although only some of the *C. cancellata* consumed by the other two species suffered similarly slight shell damage, this distinction seems insufficient to permit partitioning of field mortality among whelk species. These laboratory feeding observations imply that *B. canaliculatum* did not contribute greatly to the observed mortality of *M. mercenaria* and that Type 4 shell damage was the consequence of whelk predators. No other species of predatory gastropod was ever encountered at the site. Pooled over all whelk species, the rate of Type 4 mortality was seasonally variable. During 6 colder months from late Oct-late April, 24 *M. mercenaria* and 16 *C. cancellata* experienced Type 4 deaths, whereas during the 4 warmer months from late April-late August, 45 *M. mercenaria* and 42 *C. cancellata* deaths were assigned to Category 4 in the laboratory mortality data.

Category 5 shell damage is typical of crabs (Carriker, 1951; Landers, 1954; Vermeij, 1978). The blue crab *Callinectes sapidus* was the most evident crab at the study site and reproduced clam mortality and shell damage in the laboratory identical to that classified as Type 5. Other crabs such as *Menippe mercenaria* and small xanthids also occurred at the field site and probably also contributed to Category 5 mortality.

Mortality that produces no shell damage (Category 3) is the consequence of either disease, starvation, physiological stress, parasitism, micro-predation, senescence, or subtle attack by a large predator. No attempt was made in this study to distinguish among these possibilities.

Clams are lost (Category 2) by (1) sampling error, (2) emigration, (3) predation by shell-removing predators, or (4) post-mortem removal by scavengers. The level of sampling error was estimated by resampling in the usual fashion 13 enclosures which 24 h previously on Oct 19, 1977 had been sampled and then stocked with known numbers of marked clams in a complete array of sizes. Of 146 *Mercenaria mercenaria* recovery was 99% (1 clam missing), whereas of 143 *Chione cancellata* recovery was 96% (6 clams missing). No whelks were found in these 13 enclosures before or after the 24-h period. These data imply that sampling error was small, at least for live clams. Distinctions among the 3 remaining possibilities may often be made by a properly designed and successful caging experiment.

Caging Experiment

I developed this caging experiment to attempt to explain the disappearance of clams from the density enclosures, to test whether survivorship of both clam species would be substantially increased in the absence of whelks and other large predators, and to test whether in the absence of predation any other density-dependent mortality response (such as starvation) appeared. I constructed complete cages designed to exclude all large (> 6 mm) predators by adding 6-mm mesh VEXAR tops to enclosures identical to those used in the density manipulations. Because whelks entered enclosures by burrowing beneath the enclosure walls, I buried the walls of a complete cage to a 13–14 cm depth. The top of such an exclusion cage was kept above the sediment surface by implanting 3 wooden dowels into the sediments as internal supports for each cage roof. To control for any artifactual effects of adding the cage top, I constructed partial cages by affixing two VEXAR strips to each enclosure so as to cover half of the enclosure top. The middle was left open and the enclosure walls retained at a 10-cm depth. These partial cages allowed predators access to their prey while including a substantial amount of roofing material to reproduce at least partially any artifactual effect caused by roofing. Each cage control included 2 wooden dowels implanted into the sediments to maintain the partial tops above the sediment surface. The assumption that predators have unrestricted access to partial cages can be tested by comparing predator-related mortality inside partial cages to that inside control enclosures.

This caging experiment ran simultaneously with the second density manipulation, from July to Nov 1978, in the same matrix of enclosures. I used 2 replicates of each cage type to enclose clams at each of two densities, (1 X, 1 X) and (4 X, 4 X). Two uncaged enclosures at each of these two densities served as controls. To estimate the effects of the enclosures (especially whether the enclosures restricted access of predators), I introduced clams into unenclosed 1-m^2 field plots, marked by rebar posts at each corner. I established 2 replicates of the (4 X, 4 X) and 4 replicates of (1 X, 1 X) clam densities in unenclosed plots. Except for the presence of an enclosure, all plots were initially treated and subsequently sampled in the same fashion, identical to the procedures used for the density manipulations. Unlike the density manipulation treatments which were assigned at random to field locations, the caging treatments were grouped (with one complete cage, one partial cage, one control enclosure, and one or two unenclosed plots, depending upon density treatment) into 2 (1 X, 1 X) and 2 (4 X, 4 X) sets.

Effects of Seagrass on Clam Survivorship

To test the hypothesis that dense seagrass helps protect *Mercenaria mercenaria* and *Chione cancellata* from predation, I excavated two sets of 12 haphazardly located 1-m^2 plots in the naturally vegetated, undisturbed perimeter of the experimental matrix. All seagrass material, clams, and macrofauna were removed in a fashion identical to that used in the initial sampling. One set of samples was collected in June 1978, just after the termination of the first density manipulation experiment and just before the start of the second. The second set of grass bed samples was taken in Nov 1978, following excavation of the second density manipulation. Because the density manipulation experiments were conducted in plots from which seagrass had been removed and did not grow back during either experiment, a comparison of the fate of marked clams in those plots to clams left in the continuously vegetated, control plots around the perimeter of the experimental area provides a means of assessing the effects of dense seagrasses on survivorship of *M. mercenaria* and *C. cancellata.*

Results

Initial Biological Sampling and Physical Parameters

Seagrass was not uniformly distributed within the meadow of *Halodule wrightii* (Table 1). Separate ANOVA's performed on log-transformed above-ground and below-ground wet weights of harvested seagrass demonstrate statistically significant heterogeneity ($P < 0.001$ in both analyses) across the 3 visually determined cover categories. Preplanned Scheffé contrasts reveal that the mean wet wts of below- and above-ground seagrass were significantly lower in unvegetated plots than in partially vegetated plots ($P < 0.001$ in both comparisons) and significantly higher in thickly vegetated than in partially vegetated plots ($P < 0.05$ in both comparisons). Consequently, the visual estimations of seagrass cover served adequately to characterize both above- and below-ground patterns of seagrass abundance.

Densities of both *Mercenaria mercenaria* and *Chione cancellata* in the initial 57 1-m^2 samples (Table 1) were strongly and positively associated with seagrass abundance. Both bivalves possessed a similar relationship to seagrass abundance with separate ANOVA's on log-transformed abundances revealing statistically significant differences ($P < 0.001$ in both analyses) in abundances across seagrass cover categories. Preplanned Scheffé contrasts demonstrate that for each species average density was significantly lower ($P < 0.01$) in unvegetated plots than in partially vegetated plots and significantly higher ($P < 0.01$) in thickly vegetated than in partially vegetated plots.

Sediment penetration was more difficult in dense vegetation than in unvegetated locations (Table 1). The aver-

Table 1. Average biological and sedimentary parameter values (± 1 SE) at three different levels of seagrass abundance. Clam abundances come from 57 1-m^2 samples taken in Sept and Oct 1977 from a meadow of *Halodule wrightii* in Bogue Sound, NC: 9 unvegetated, 20 partially vegetated, and 28 thickly vegetated plots. Seagrass wet weights come from the first four 1-m^2 samples in each seagrass cover category. Sediment data taken from identical study site in April 1981. A dash indicates data not available

Parameter	Seagrass cover categories		
	Unvegetated	Partially vegetated	Thickly vegetated
Wet weight of seagrass (g m^{-2})			
(a) Above ground ($n=4$)	1.2 (±0.7)	390 (±108)	1103 (±166)
(b) Below ground ($n=4$)	11.8 (±3.1)	375 (±99)	867 (±117)
Density of *Mercenaria mercenaria* (no. m^{-2})	0.4 (±0.4)	4.2 (±1.0)	11.3 (±1.7)
Density of *Chione cancellata* (no. m^{-2})	0.4 (±0.2)	5.2 (±1.3)	10.3 (±1.2)
Rod penetration depth in cm ($n=6$)	4.1 (±0.1)	–	0.5 (±0.1)
Number of penetrometer taps needed to penetrate 10 cm ($n=6$)	11.9 (±2.0)	–	26.0 (±3.9)
% silt-clay by weight ($n=3$)	1.04 (±0.1)	–	2.66 (±0.5)

age distance penetrated by the penetrometer rod before tapping and the average number of taps required to produce a 10-cm penetration both differed significantly ($P < 0.01$ in Student's t-tests) between vegetated and unvegetated plots. Despite this difference, sediment size distributions by weight were similar with 82.3% in the seagrass and 84.1% in the sand in the fine sand size class (0.125–0.250 mm). The seagrass sediments possessed a slightly higher silt-clay content (Table 1).

Density Manipulations

For *Mercenaria mercenaria* and *Chione cancellata,* the intra- and interspecific effects of density on (1) survivorship of marked clams, (2) percent missing, and (3) percent dead with rasped shells (from whelk predation) were evaluated separately for each density manipulation experiment by 2-way ANOVA without replication on angular-transformed proportions (2 arcsin $\sqrt{P}$). In no test was the response to density significant at a 5% level of significance. Table 2 presents the marginal totals, pooled across all interspecific densities for each species in each experiment, to illustrate how *M. mercenaria* and *C. cancellata* were unaffected by varying intraspecific density.

Table 2. *Mercenaria mercenaria* and *Chione cancellata.* Percent survivorship and mortality by source as a function of intraspecific density in two successive experiments Oct 77 – May 78 and July – Nov 78 wherein densities of *M. mercenaria* and *C. cancellata* were varied in a factorial design. No: the number of individuals at the start of the experiment, A: percent alive at the end, M: percent missing, DU: percent dead with undamaged shells, and DW: percent rasped by whelks. Data are marginal totals pooled across all interspecific densities. 1X density was 7 m^{-2} for both species. A dash indicates data not available

Intra-specific density	Experiment 1					Experiment 2				
	No	A	M	DU	DW	No	A	M	DU	DW
(a) *Mercenaria mercenaria*										
1/4 – 1/2X	20	60	10	0	30	8	13	0	0	88
1X	35	29	31	0	40	28	0	29	0	71
2X	70	41	29	0	30	–	–	–	–	–
4X	140	44	18	0	39	112	3	16	0	80
(b) *Chione cancellata*										
1/4 – 1/2X	20	25	40	0	35	8	25	38	0	38
1X	35	20	54	3	23	28	11	29	0	61
2X	70	14	49	4	33	–	–	–	–	–
4X	140	16	49	2	33	112	1	20	5	74

ANOVA may be an overly conservative means of testing the statistical significance of density effects on these mortality and survivorship data because proportions calculated from low-density treatments, with sample sizes here as small as 2 for ¼ X and 4 for ½ X treatments, are weighted equally with proportions calculated from higher-density treatments. An alternative statistical approach is provided by χ^2 contingency tests of independence, performed on marginal totals, pooled across all interspecific (or intraspecific) densities. In such a χ^2 test, each individual clam is treated as an independent replicate, which has the effects of weighting the density treatments in proportion to the clam density within them and of ignoring the variability among replicate enclosures at any given intraspecific (or interspecific) density.

Application of χ^2 contingency tests generally confirms the results of the more conservative ANOVA's. In χ^2 tests on the pooled totals of the 2 density manipulation experiments, only one effect of intraspecific density was significant ($P < 0.05$): survivorship of *Chione cancellata* declined with increasing density. The less conservative χ^2 tests serve to demonstrate that for both *Mercenaria mercenaria* and *C. cancellata* an apparent trend of increasing rates of whelk predation with density (Table 2) is not statistically significant. The pattern of whelk predation on *M. mercenaria* (percent taken by whelks changing from 47% at an intraspecific density of ¼–½ X to 54% at 1 X and to 57% at 4 X) is likely to have occurred by chance alone ($P > 0.20$). Similarly, the *C. cancellata* pattern (percent taken by whelks changing from 36% at ¼–½ X to 40% at 1 X and to 51% at 4 X) is non-significant ($P > 0.10$).

Table 3. Percent survivorship and mortality by source as a function of size for *Mercenaria mercenaria* in two successive experiments wherein densities of *M. mercenaria* and *Chione cancellata* were varied in a factorial design. No: the number of *M. mercenaria* at the start of the experiment, A: percent alive at the end, M: percent missing, DU: percent found dead with undamaged shells, and DW: percent rasped by whelks. Data presented by size class pool the results over all densities. Statistical significance in contingency tests of size independence indicated by superscripts on totals[a]

Size class (cm)	No	A	M	DU	DW
(a) Experiment 1 – Oct 77 – May 78					
0.60 – 3.99	100	43	41	0	16
4.00 – 5.99	64	38	16	0	47
6.00 – 7.99	63	41	10	0	49
≧8.00	38	53	0	0	47
Total	265	43	22***	0	36***
(b) Experiment 2 – July – Nov 78					
0.60 – 3.99	39	8	38	0	54
4.00 – 5.99	32	3	16	0	81
6.00 – 7.99	39	0	13	0	87
≧8.00	38	0	3	0	97
Total	148	3	18***	0	80***

[a] *** $P < 0.001$, no notation $P > 0.05$

Table 3 (for *Mercenaria mercenaria*) and Table 4 (for *Chione cancellata*) present the fate of all marked clams in the unvegetated enclosures during each density manipulation experiment as a function of clam size. The totals across all sizes illustrate clearly the low rates of clam survivorship during these experiments and the importance of whelks to that process. In the first experiment, 36% and, in the second experiment, 80% of marked *M. mercenaria* were recovered as rasped, empty shells. A similar pattern was exhibited by *C. cancellata* with 32 and 70% of marked clams in the two experiments found dead with whelk-damaged shells. These percentages, although large, are underestimates of the true losses to whelks because all clams eaten by whelks were not necessarily recovered during sampling. Whelk predation was more intense on both clam species during the second experiment which, although shorter, included more warm-water months during which the whelks held in the laboratory (see Materials and Methods section) were more active clam consumers. The patterns and rates of survivorship and mortality were similar for the 2 clam species, except that (1) *C. cancellata* had a higher rate of disappearance and correspondingly lower survivorship than *M. mercenaria* in the first experiment and (2) *C. cancellata* exhibited mortality which left no shell damage.

Table 4. Percent survivorship and mortality by source as a function of size for *Chione cancellata* in two successive experiments wherein densities of *Mercenaria mercenaria* and *C. cancellata* were varied in a factorial design. No: the number of *C. cancellata* at the start of the experiment, A: percent alive at the end, M: percent missing, DU: percent found dead with undamaged shells, and DW: percent rasped by whelks. Data presented by size class pool the results over all densities. Statistical significance in contingency tests of size independence indicated by superscripts on totals[a]

Size class (cm)	No	A	M	DU	DW
(a) Experiment 1 – Oct 77 – May 78					
0.60 – 2.49	60	13	68	7	12
2.50 – 3.49	194	18	43	2	37
≧3.50	11	9	45	0	45
Total	265	17	49*	3	32**
(b) Experiment 2 – July – Nov 78					
0.60 – 2.49	3	67	33	0	0
2.50 – 3.49	47	6	30	2	62
≧3.50	98	1	18	5	76
Total	148	4*	22	4	70**

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, no notation $P > 0.05$

The statistical significance of the effects of clam size on percent survivorship and rate of each type of mortality was assessed by successive χ^2 contingency tests of independence on the data in Tables 3 and 4. Before testing, the small and medium size classes of *Chione cancellata* were combined in the second experiment because of insufficient sample size (3) in the small size class. Following Snedecor and Cochran (1969), Fisher's exact test was used to assess significance in instances where an expected value fell below unity (all tests on rate of mortality which left undamaged shells, DU, and the test on *Mercenaria mercenaria*'s survivorship in the second experiment, A). Although contingency tests of size dependency on data pooled over all replicates ignore variations among replicate enclosures, this is an appropriate statistical test because initial size frequency distributions were identical across all enclosures, thus rendering each size class equally available to any enclosure-specific event. Successive contingency tests on the same survivorship and mortality data are not independent: for instance, a significant effect of any mortality agent is likely to produce a complementary effect on survivorship, and loss of clams to one type of mortality will render fewer individuals available to suffer loss from another source.

Contingency tests on *Mercenaria mercenaria* data (Table 3) reveal a highly significant ($P < 0.001$) effect of clam size on percent missing and on percent eaten by whelks in each experiment. These effects of size were complementary, with smaller clams more likely to disappear and larger ones more likely to fall prey to whelks. Because these two size effects were nearly balanced, survivorship never depended upon clam size in *M. mercenaria*.

Whelk predation on *Chione cancellata* also increased significantly ($P < 0.01$) with clam size in both experiments (Table 4). The largest *C. cancellata* (4.4 cm in length) and the largest *Mercenaria mercenaria* (13.3 cm) individuals used were consumed by whelks. As in *M. mercenaria*, percent missing declined with increasing size in *C. cancellata*, although the effect was significant ($P < 0.05$) in only the first experiment. In the second experiment, *C. cancellata* exhibited a significant ($P < 0.05$) decline in percent survival with increased size as an apparent consequence of the high intensity of whelk predation on larger clams.

Table 5. Percent survivorship and mortality pooled across two densities (1 X and 4 X) for *Mercenaria mercenaria* and *Chione cancellata* from July to Nov 78 in: (1) enclosures covered with a 6-mm mesh complete top (full cages), (2) half-covered (cage controls) enclosures, (3) uncovered (controls) enclosures, and (4) unenclosed plots. No: the number of clams at the start of the experiment, A: percent alive at the end, M: percent missing, DU: percent found dead with undamaged shells, DW: percent rasped by whelks, and DC: percent crushed or chipped by crabs. 1 X density was 7 m^{-2}

Treatment	No	A	M	DU	DW	DC
(a) *Mercenaria mercenaria*						
Full cages	68	91	4	1	3	0
Cage controls	69	16	9	1	72	1
Controls	70	6	17	0	77	0
Unenclosed plots	84	2	31	0	67	0
(b) *Chione cancellata*						
Full cages	70	74	7	17	0	1
Cage controls	70	16	23	9	53	0
Controls	70	4	17	3	76	0
Unenclosed plots	84	5	23	7	65	0

Responses to Caging

Results of the caging experiment, pooled across all 1 X and 4 X density treatments, appear in Table 5. Pooled totals are presented because neither clam species exhibited any significant response (at $P < 0.05$) to density within any treatment type (using χ^2 contingency and Fisher's exact tests of independence to compare survivorship and loss to each mortality type). These comparisons included a test of whether the loss to mortality agents which leave undamaged shells increased with density inside complete exclusion cages. Because starvation is included among the potential contributors to mortality of this type, the lack of density dependence in this category implies that in the absence of predators density dependent starvation did not occur within the fourfold range of densities used during this 4-mo experiment.

For *Mercenaria mercenaria* and *Chione cancellata*, the significance of caging treatments on (1) survivorship (A), (2) disappearance rate (M), (3) death rate by agents leaving unmarked shells (DU), and (4) death rate by whelks (DW) was evaluated by successive 1-way ANOVA's on angular-transformed proportions (2 arcsin $\sqrt{P}$). Whenever the ANOVA proved significant, 3 Scheffé preplanned contrasts were calculated to determine the significance of differences between (1) unenclosed plots and enclosed controls, (2) enclosed controls and cage controls, and (3) cage controls and complete exclusion cages (Table 6). Because low density (1 X) treatments produce inherently more variable proportion data, yet are weighted equally with high density (4 X) treatments in estimating the error variance in these ANOVA's, this test is again conservative. A second, less conservative test is provided by contingency tests (χ^2, except where low expected values required Fisher's exact test) done on the totals pooled over all replicates, testing the significance of each of the same between-treatment comparisons made by the Scheffé contrasts (Table 6). Such contingency tests weight each individual clam equally but are thereby largely determined by the behavior of the high-density replicates.

Both statistical approaches demonstrate that enclosing the clams had very little effect on survivorship or on type and rate of mortality (Tables 5, 6). In all the Scheffé and contingency test comparisons between unenclosed

Table 6. Results of ANOVA's and χ^2 tests of significance on *Mercenaria mercenaria* and *Chione cancellata* mortality and survivorship data summarized in Table 5. Significance levels given in ANOVA columns are derived from Scheffé preplanned contrasts performed only when overall ANOVA done on angular-transformed proportions was significant. χ^2 tests done on pooled totals of all replicates

Species and treatments compared	Statistical significance[a, b] of between-treatment difference in:							
	Survivorship (% A)		Missing rate (% M)		Death rate leaving undamaged shells (% DU)		Whelk predation rate (% DW)	
	ANOVA	χ^2	ANOVA	χ^2	ANOVA	χ^2	ANOVA	χ^2
(a) Comparison of unenclosed plots and controls (testing enclosure artifacts)								
M. mercenaria	ns	ns	ns	*	ns	ns	ns	ns
C. cancellata	ns	ns	ns	ns	ns	ns	ns	ns
(b) Comparison of controls and cage controls (testing cage artifacts)								
M. mercenaria	ns	ns	ns	ns	ns	ns	ns	ns
C. cancellata	ns	*	ns	ns	ns	ns	ns	**
(c) Comparison of cage controls and full cages (testing the effects of predators)								
M. mercenaria	***	***	ns	ns	ns	ns	**	***
C. cancellata	**	***	ns	**	ns	ns	**	***

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns $P > 0.05$

[b] in ANOVA's *M. mercenaria* showed significance of caging on survivorship ($P < 0.001$) and whelk predation ($P < 0.01$), while *C. cancellata* showed significance of caging on survivorship ($P < 0.001$) and whelk predation ($P < 0.001$). No other ANOVA was significant

plots and control enclosures (line a, Table 6), only one significant difference appeared: in the χ^2 test, disappearance rate of *Mercenaria mercenaria* was higher ($P < 0.05$) outside of enclosures, as would be expected if enclosure walls were necessary to restrict lateral movement of the clams. This difference is not confirmed by the ANOVA but is probably real because an ANOVA on the 4 X treatments alone is significant ($P < 0.01$) and a Scheffé contrast reveals a significantly ($P < 0.05$) higher loss rate outside of enclosures. The presence of enclosure walls played no role in affecting the rate of whelk predation, probably because these gastropods are such adept diggers in the top 10 cm of fine sands.

In comparing the cage controls to the control enclosures (line b, Table 6), agreement between the two statistical approaches is again generally good. Both statistical tests demonstrate no effect of the addition of a partial cage top on survivorship or mortality rates of *Mercenaria mercenaria.* For *Chione cancellata,* the Scheffé contrasts reveal no significant effect of partial roofing on any of the survivorship and mortality categories, whereas χ^2 contingency tests show that whelk predation was reduced ($P < 0.01$) and survivorship increased ($P < 0.05$) by addition of partial roofing.

The disagreement between the two statistical approaches does not require resolution because the magnitude of these possible cage artifacts on *Chione cancellata's* survivorship and rate of death by whelks is small compared to the effects of adding a complete cage top (Table 5). Both statistical tests demonstrate the highly significant ($P < 0.01$ or $P < 0.001$) effects of adding a complete cage top and extending the depth of walls on the rate of whelk predation on and survivorship of both *Mercenaria mercenaria* and *C. cancellata* (line c, Table 6). Installing full cages effectively excluded whelks, reducing the loss to whelks from 53–77% in controls to 0–3% inside exclusion cages. In the absence of whelk predation, survivorship of both species was high (Table 5).

The χ^2 contingency test reveals a significantly lower ($P < 0.01$) rate of *Chione cancellata* disappearance inside full cages than in cage controls (Table 6). If real, such a difference could arise either from inhibition of clam migration by the deeper walls or from exclusion of large, shell-removing predators and scavengers by the complete top. Although neither test revealed a significant difference in disappearance of *Mercenaria mercenaria* between full and partial cages, evidence that both species occasionally escaped the enclosures comes from recovery of painted clams (6 *M. mercenaria* and 8 *C. cancellata*) alive and outside of assigned enclosures.

The whelks encountered during sampling of the density manipulation and caging experiments provide an indication of the relative abundances of the separate species. The initial excavation of 57 1-m^2 plots produced 3 *Busycon carica* and 2 *B. canaliculatum.* These 5 whelks were evenly distributed over the initial sampling period, with 2 in the first 19 samples (Sept 27–Oct 4), 2 in the next 19 samples (Oct 5–6), and 1 in the last third of the samples (Oct 6–11). The final sampling in Nov 1978 of 39 1-m^2 enclosures, unenclosed plots, and partial cages produced 5 *B. carica,* 3 *B. contrarium,* and 6 *B. canaliculatum.* No *B. canaliculatum* was observed in the process of rasping or feeding on a clam (perhaps because of the species' nocturnal habits, Paine, 1962), whereas most other whelks encountered were attacking a *Mercenaria mercenaria* or a *Chione cancellata.*

Effects of Seagrass on Clam Survivorship

Fig. 1 shows the temporal changes in average densities of *Mercenaria mercenaria* and *Chione cancellata* in both sets of experiments and in the still vegetated grass bed perimeter. To avoid any confounding density effects, average clam densities plotted for the two sets of experiments include only those enclosures where clam densities were retained at 1 X density (7 m^{-2}): 14 in Experiment 1 (5 1 X enclosures in the factorial matrix, 5 additional (1 X, 1 X) enclosures, and 4 (1 X, 1 X) controls in unenclosed 1-m^2 plots) and 9 in Experiment 2 (4 1 X enclosures in the factorial matrix, 1 additional (1 X, 1 X) enclosure, and 4 (1 X, 1 X) controls in unenclosed 1-m^2 plots). Initial average densities in the two experiments have zero variance because total density of marked clams was set at a constant 7 m^{-2} in all 1 X plots. Final densities include all marked clams recovered, all immigrants, and all new recruits. Average clam densities in the seagrass bed are based upon the initial (Oct 1977) 57 1-m^2 samples and 2 sets of 12 1-m^2 samples distributed around the still vegetated perimeter of the experimental area in June 1978 and Nov 1978.

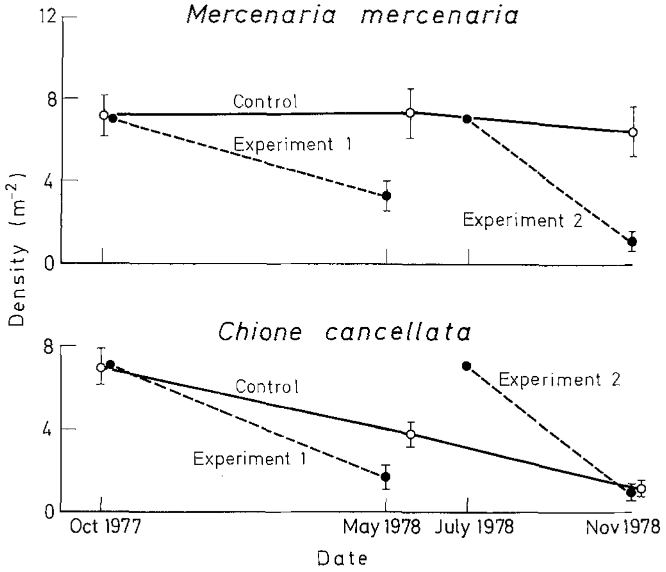

Fig. 1. Changes in *Mercenaria mercenaria* (top graph) and *Chione cancellata* (bottom) densities in 1-m^2 fixed plots from which seagrass has been experimentally removed (Experiments 1 and 2) and in samples from the surrounding, still vegetated control area. Abundances inside the fixed plots (14 in Experiment 1 and 9 in Experiment 2) were initially set at a constant 7 marked clams m^{-2}. Final densities include marked clams plus any new recruits or immigrants. Density inside grass bed area was estimated by haphazard 1-m^2 samples (57 in Oct 1977, 12 in June 1978, and 12 in Nov 1978). Bars mark off ± 1 SE

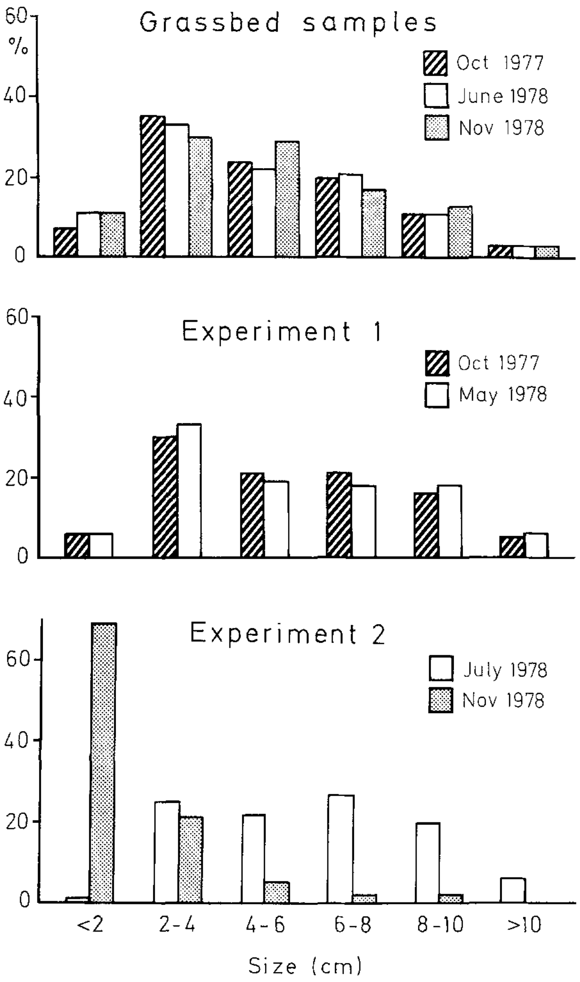

Fig. 2. Temporal changes in *M. mercenaria* size frequencies: (1) (top) within the control *Halodule wrightii* bed from Oct 1977 (405 clams) to June 1978 (87 clams) to Nov 1978 (77 clams), (2) (middle) during the first density manipulation experiment from Oct 1977 (468 clams) to May 1978 (232 clams), and (3) (bottom) during the second density manipulation experiment from July 1978 (267 clams) to Nov 1978 (27 clams). χ^2 goodness of fit tests demonstrate no significant change in size distribution in (1) ($\chi^2 = 4.01$, $0.90 < P < 0.95$) and (2) ($\chi^2 = 1.89$, $0.80 < P < 0.90$) but a significant shift in (3) ($\chi^2 = 192.4$, $P < 0.001$)

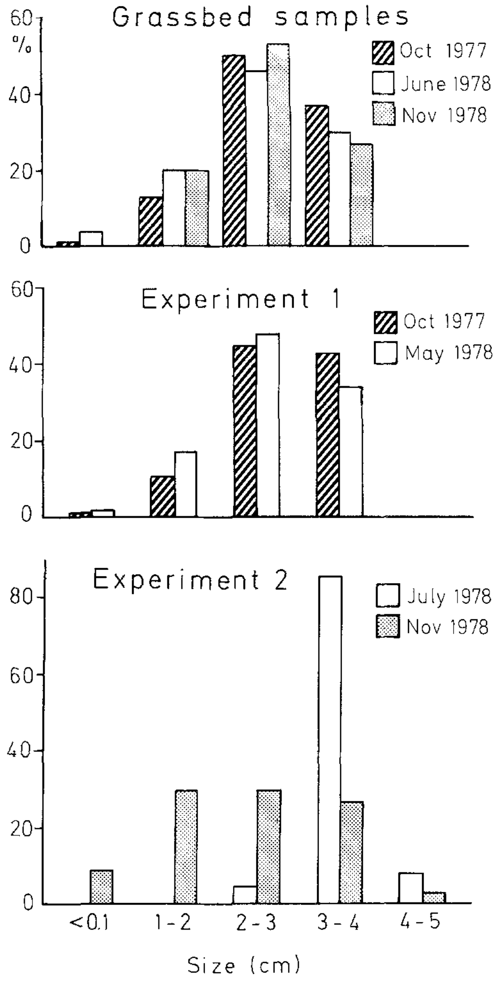

Fig. 3. Temporal changes in *C. cancellata* size frequencies: (1) (top) within the control *Halodule wrightii* bed from Oct 1977 (389 clams) to June 1978 (46 clams) to Nov 1978 (15 clams), (2) (middle) during the first density manipulation experiment from Oct 1977 (468 clams) to May 1978 (106 clams), and (3) (bottom) during the second density manipulation experiment from July 1978 (267 clams) to Nov 1978 (25 clams). χ^2 goodness of fit tests demonstrate no significant change in size distribution in (1) ($\chi^2 = 5.62$, $0.40 < P < 0.50$) and (2) ($\chi^2 = 5.06$, $0.10 < P < 0.20$) but a significant shift in (3) $\chi^2 = 132.9$, $P<0.001$)

In the grass bed perimeter, the density of *Mercenaria mercenaria* remained constant (Fig. 1) both during the Oct–June and June–Nov periods ($P > 0.05$ in both Student's *t*-tests). In contrast, total abundance of *M. mercenaria* inside the unvegetated 1 X experimental plots declined by 54% during the first experiment and by 84% during the second experiment. At the termination of each experiment, the average density of *M. mercenaria* was significantly lower in the 1 X experimental plots than in the control samples from the surrounding seagrass bed (Student's *t*-test: $P < 0.01$ in Experiment 1 and $P < 0.001$ in Experiment 2). *Chione cancellata* demonstrated a similar pattern: in the vegetated control area, the average density of *C. cancellata* declined significantly ($P < 0.01$) by 45% from Oct 1977 to June 1978 and by 67% from June 1978 to Nov 1978 (Fig. 1). The decline in *C. cancellata* abundance in the 1 X experimental plots was even greater: 76% in the first experiment and 84% in the second experiment. At the termination of the first experiment, the density of *C. cancellata* in 1 X plots was significantly ($P < 0.01$ in a Student's *t*-test) lower than in the grass bed controls despite equivalent initial densities. During the second experiment, despite initially higher density in the experimental 1 X plots ($P < 0.001$ in a Student's *t*-test), the density of *C. cancellata* at the end of the second experiment in Nov 1978 did not differ significantly between the grass bed and the 1 X experimental plots.

Figs. 2 and 3 provide size frequency histograms for all *Mercenaria mercenaria* and *Chione cancellata*, respectively, collected in the three sets of grass bed samples (Oct 1977, June 1978, and Nov 1978) and in the experimentally unvegetated plots at the beginning and at the end of each density manipulation experiment. The histograms for the unvegetated plots include all density treatments in each density manipulation experiment. Within the seagrass bed, neither species showed any significant change in size frequency distribution over all 3 dates (tested by χ^2). In the first density manipulation experiment, no significant shift in size frequencies occurred, but during the second density manipulation, size frequency distributions of both *M. mercenaria* and *C. cancellata* shifted significantly ($P < 0.001$) towards the smaller size classes. The major cause of these size frequency changes was the more intense whelk predation on larger clams (Tables 3, 4).

These comparisons of size frequency distributions of clams inside and outside of the seagrass bed demonstrate that the higher densities maintained inside the seagrass bed (Fig. 1) were not the result of higher rates of recruitment despite equal rates of whelk predation. If recruitment had been important, size frequency distributions would have shifted more towards smaller clams in the seagrass samples than in the experimental plots. Figs. 2 and 3 reveal that when ever size frequencies changed during these experiments, the opposite pattern was evident in which the experimental plots became relatively more enriched with smaller clams.

Discussion

From the results of previous studies demonstrating higher benthic macrofaunal abundances in seagrass beds (e.g., Santos and Simon, 1974; Thayer *et al.,* 1975; Orth, 1977; Reise, 1977; Stoner, 1980), the direct relationship between seagrass cover and the densities of *Mercenaria mercenaria* and *Chione cancellata* (Table 1) was expected. By experimentally removing the seagrass from plots within the grass bed and then comparing the fate of individually marked clams in those unvegetated plots to the behavior of clam density in the unaltered, still densely vegetated perimeter, I gathered data which suggest that in some way the presence of seagrasses insulates *M. mercenaria* and *C. cancellata* from higher mortality rates that would otherwise prevail (Fig. 1). Most of the mortality in the unvegetated plots appeared to result from whelk predation from *Busycon carica, B. contrarium,* and possibly *B. canaliculatum* (Table 2). Seagrass thus appears to provide the structural habitat heterogeneity that serves *M. mercenaria* and *C. cancellata* as a refuge from whelk predation.

Although the physical disturbance from cage and enclosure installation and initial sampling may have contributed to the higher rates of whelk predation in the experimentally unvegetated enclosures, it is unlikely that such a disturbance artifact was the major cause of the observed between-habitat differences. Despite intense physical disturbance during 3 wk of enclosure installation, the numbers of whelks from inside enclosures during the 15 d of initial sampling were uniformly distributed over the serial samples, with no tendency toward increased counts with time (data given in Responses to Caging section of Results). Although the same plot was never sampled twice during this initial sampling, a second data set (in Interpreting Clam Mortality and Loss section of Materials and Methods) provides evidence that whelks did not quickly invade specific plots immediately after sampling disturbance. The 13 1-m^2 enclosures which were resampled after 24 h to estimate sampling efficiency demonstrated no whelk immigration during that time period. Although these observations do not totally eliminate the possibility of a physical disturbance artifact, they imply that such an artifact was not a major contributor to the large between-habitat differences in clam survivorship.

Although both clam species were less vulnerable to whelk predation in the *Halodule wrightii* meadow, the two species differed in degree of protection. The density of *Mercenaria mercenaria* remained unaltered in control vegetation, whereas the density of *Chione cancellata* declined (Fig. 1). Individuals of *M. mercenaria* live perhaps 3–4 cm deeper in the sediments than *C. cancellata.* As the seagrasses and clams were excavated from the experimental plots, individuals of *M. mercenaria* were usually discovered surrounded by roots and rhizomes of seagrass, whereas specimens of *C. cancellata* appeared to live above the levels of densest root mat. Seagrass may provide less protection to *C. cancellata* from whelks because of its more shallow living depth. If so, this implies that the presence of roots and rhizomes is the significant protective feature of the seagrass plant. The amount of above- and below-ground vegetation in the initial 57 1-m^2 samples did not vary independently and the experiments were not designed to separate the effects of the below-ground components from the effects of the entire plant. However, the penetrometer data demonstrate that penetration into the fine sand sediments was more difficult in the seagrass bed (Table 1). I therefore elaborate upon the hypothesis of Ginsburg and Lowenstam (1958), Orth (1977), Virnstein (1977), and Reise (1977, 1978) by proposing that the roots and rhizomes of the seagrass function as a refuge by binding the sediments and thereby increasing sediment compaction. Although I possess only physical data from the penetrometer, digging by whelks and other predators may be similarly inhibited by the presence of seagrasses.

Other studies have attempted to test the hypothesis that seagrass provides the infauna a partial refuge from predation. In the laboratory, Reise (1977) demonstrated that the shore crab *Carcinus maenas* L. killed fewer infauna in the presence of seagrass plants. A major difficulty with a laboratory test is insuring that the transplanted seagrasses bind the sediments to the same degree as a natural, undisturbed stand of plants. Previous attempts (Young *et al.,* 1976; Orth, 1977; Reise, 1977, 1978; Virnstein, 1977; Summerson, 1980) to test this hypothesis by using cages in the field to exclude large mobile predators suggest that predation on infauna is inhibited by natural, undisturbed stands of seagrasses; however, these results are difficult to interpret because of the influence of serious cage artifacts, including the tendency for "exclusion cages" to become enriched with predatory crustaceans (Young *et al.,* 1976; discussed by Peterson, 1979b). The results reported here test this refuge hypothesis directly in the field without disturbing the seagrass plots and without relying on cages within the seagrass habitat.

The predator-prey interaction between clams and whelks is apparently not stabilized by a density-dependent feeding response (*sensu* Murdoch and Oaten, 1975). Over the ranges of densities used (2–28 m^{-2}), there was no consistently significant effect of intra- or interspecific density on survivorship or on the rate of any type of mortality (including whelk predation) in either species of clam (Table 2). Whelks appear to select the larger sizes of both species and can and did consume even the largest clams used in this experiment (Tables 3, 4). The apparent lack of a stabilizing functional response (Holling, 1959) and of a size refuge from whelk predation (*sensu* Connell, 1970) helps to emphasize the importance of the seagrass refuge to the persistence of this predator-prey system in the fine-sand flat environment.

The areal extent of visible above-ground vegetation in North Carolina's *Halodule wrightii* and *Zostera marina* beds varies greatly during and over years. If the below-ground components remain intact for a significant time after exfoliation or death of the above-ground components, it is possible that an area of apparently unvegetated substrate could retain refuge characteristics because of continued presence of seagrass roots and rhizomes. In this way, the history of floral occupation of a locality could be extremely important in determining its present faunal densities and may contribute to the observed high spatial variability in density of shallow-water marine benthic infauna. Some of this unexplained spatial variability could perhaps be removed in future studies if subsurface macro-detritus were to be quantified and used as an independent variable to explain variation in the benthos.

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