

Role of predation in organizing benthic communities of a temperate-zone seagrass bed

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ABSTRACT: Monthly coring for 6 mo at 9 positions along a transect extending from 15 m within to 15 m outside a North Carolina (USA) seagrass bed revealed higher densities of macrobenthic animals within the vegetated area. In the seagrass, average density of epibenthos was $52 \times$ and of infauna $3 \times$ the level observed on the adjacent sand flat. Among infaunal guilds, suspension feeders responded most, predator-scavengers less, and surface- and subsurface-deposit feeders least to the presence of seagrass. Caging with 6 mm mesh for successive 2 mo periods in the seagrass had a small and statistically non-significant effect on macro-infaunal density. In analogous sand-flat experiments, the total infaunal density was substantially higher under full cages than in uncaged controls. Under partial cages, used as cage controls, infaunal densities were indistinguishable from those observed in uncaged controls, implying that predation by large (> 6 mm) epibenthic consumers rather than cage artifacts was the major cause of the response of infauna to caging. Among infauna, only the suspension-feeder guild exhibited a significant cage artifact, which in combination with a large effect of predator exclusion may explain its relatively large response to seagrass. Relative and absolute responses of separate infaunal guilds to caging closely matched their responses to the presence of seagrass. Total infaunal densities inside full cages on the sand flat increased to levels indistinguishable from those observed at the same times in the seagrass bed, implying that predation by large epibenthic consumers was the major cause of the observed between-habitat differences in infaunal densities. Average species diversity (H'), richness (S), and evenness (J') per core changed along the transect from sand flat to seagrass bed and underneath cages on the sand flat as predicted by a simple species-individual curve. This implies a lack of competitive exclusion where macrobenthic densities were partially released from epibenthic predation. Seining revealed large numbers of epibenthic predators inside seagrass beds and few, if any, on unvegetated flats except at night. We propose that epibenthic predators remain inside seagrass beds and other refuges during daylight and restrict their predation on sand-flat infauna to the night, when risk of higher-order predation is reduced. This hypothesis implies that the importance of epibenthic predation on the infauna should decline as a function of increasing distance from the nearest seagrass-bed refuge.

INTRODUCTION

In temperate and subtropical embayments, benthic invertebrates sampled by corers, grabs, or bottom dredges characteristically exhibit higher densities and species diversities within seagrass beds than in nearby unvegetated sediments. This general pattern is based upon studies of temperate eelgrass (*Zostera* spp.) beds in Japan (Kikuchi, 1966), southern California (Warne, 1971), North Carolina (Thayer et al., 1975), the Chesapeake Bay (Orth, 1977), and the Wadden Sea (Reise, 1977), as well as by subtropical turtlegrass (*Thalassia* spp.) and shoalgrass (*Halodule* spp.) systems (O'Gower and Wacasey, 1967; Santos and Simon,

1974; Brook, 1978; Stoner, 1980; Peterson, 1982). The single tropical study presently available also follows this same pattern (Taylor and Lewis, 1970). One hypothesis to explain this pattern is that invertebrate larvae and/or suspended food are trapped by the baffling action of emergent blades (e.g. Tegner and Dayton, 1981). An alternative explanation contends that the physical presence of seagrass blades, roots and rhizomes inhibits the effectiveness of various predators and thereby permits a release of benthic densities and diversities from the usual predatory controls operating in unvegetated sediments (Heck and Wetstone, 1977; Orth, 1977; Nelson, 1979; Peterson, 1979, 1982; Stoner, 1980, 1982; Heck and Thoman, 1981).

This differential-predation hypothesis finds support in caging experiments which demonstrated that experimental exclusion of large mobile predators, such as crabs and fishes, has a large effect on benthic communities in unvegetated sediments (Virnstein, 1977; Reise, 1977, 1978; Holland et al., 1980) but little or no impact on the benthos in seagrass beds (Young et al., 1976; Orth, 1977; Reise, 1977, 1978; Virnstein, 1978; Young and Young, 1978). Because of the possible confounding contributions of numerous uncontrolled artifacts of caging (Virnstein, 1978; Peterson, 1979; Hulberg and Oliver, 1980; Dayton and Oliver, 1980), unequivocal interpretation of these results is difficult. Consequently, we designed a parallel set of caging experiments in unvegetated bottom and in an adjacent seagrass bed, in which we included partial cages to serve as controls for possible cage artifacts. We further tested the differential-predation hypothesis by subdividing the benthos into several ecological types, based upon living position and trophic status, and comparing the separate responses of each type following caging to their responses to the presence of seagrass as a means of separating potentially competing explanations of the caging results.

MATERIALS AND METHODS

Study site

The study site was in Back Sound, Carteret County, North Carolina (USA) along the southern edge of Middle Marsh, a relict flood-tidal delta. This locale is isolated and relatively pristine. At the nearby (4 km) Duke University Marine Laboratory, over a 4 yr period water temperature varied seasonally from about 2 °C in February to 30 °C in August, whereas salinities varied in a less predictable pattern over a range of about 18 to 37 ‰ (Sutherland and Karlson, 1977). The shallower areas of Middle Marsh probably experience somewhat greater extremes in both temperature and salinity. The specific study site used was rarely subjected to strong water currents or to large waves because of its protection by the land mass of Middle Marsh with its dense cover of *Spartina alterniflora*.

We studied one particular locality where a seagrass bed, composed of a mixture of eelgrass *Zostera marina* and shoalgrass *Halodule wrightii*, extended from the low intertidal zone to the edge of a slightly deeper, subtidal, fine-sand flat. We confined all our sampling and experimentation to the shallow subtidal portions of this locality. During the study period of May–December 1977, the above-ground extent of the seagrass bed showed no obvious change despite the characteristic partial exfoliation of *Z. marina* during

August. The typical length of the seagrass blades remained about 30 cm and the seagrass blade density about 600 to 1200 m⁻².

Benthic sampling

To test whether the density and sample species diversity of sedentary macrobenthos at our study site varied significantly with the presence of seagrasses, we took core samples approximately monthly from June to December 1977 along a transect perpendicular to the edge of the seagrass bed and extending from 15 m inside the bed to 15 m outside. We first inserted metal poles into the substrate projecting ~ 20 cm above the surface at each position along the transect: one at the edge of the seagrass bed, and others at 1, 5, 10, and 15 m in each direction. One sample was then taken at each position on each of 6 sampling dates: 2 June, 28 July, 24 August, 1 October, 7 November, and 17 December, totaling 54 separate cores. Sampling effort was distributed in this fashion to maximize spread across time and space (positions along the transect). Although, with only one sample at each time and location, we sacrificed ability to detect significant temporal variation at any given location or spatial variation on any given date, we maximized the spread of our sampling and thus the generality of our test of whether the presence of seagrasses affects the macrobenthos. The precise location of each sample was at a fixed distance away from the marker stake in a direction parallel to the edge of the seagrass bed: this distance was chosen at random for each sampling visit and for each position and was constrained to fall at whole meter intervals in a range of 1 to 6 m. No sample was taken on a spot which had been sampled previously. Because samples were taken at least 1 m away from the marker poles, we doubt that the presence of the poles had an effect. The densities and diversities at the 1 m position show no tendency towards being higher or lower than the averages of all the other 5 positions in the seagrass or on the sand flat.

To sample the benthos, we inserted, stoppered, and withdrew a cylindrical Plexiglas corer with inner diameter 12.4 cm (covering 121 cm² in surface area) to 25 cm depth. Contents of the corer were sieved in the field through 1.2 mm mesh. We chose this mesh size because of our focus on not only the larger predators but also the larger prey, which contribute the majority of biomass in the system. Sampling the macrobenthic species in this vicinity with 0.5 mm mesh would have increased densities by a factor of about 2, whereas sampling with 0.062 mm would have increased infaunal densities by a factor of about 10 (J. H. Hunt, pers. comm.). Each sieved sample was cooled to 4 °C to

reduce fragmentation of polychaetes, stained with rose bengal, and preserved in buffered 10 % formalin. After at least 24 h, samples were passed through a 6.1 mm sieve to separate fresh seagrasses from detritus and to facilitate separation of benthic invertebrates from the vegetation. All fresh seagrass material (including roots and rhizomes) retained on the 6.1 mm mesh was removed and dried at 105 °C to constant weight. The invertebrates were stored in 70 % ethyl alcohol until identification. Except for (infrequent) nemerteans, burrowing anemones, polyclads, oligochaetes and hemichordates, identification proceeded to the species level.

Sediment sampling and analysis

On 10 October 1977, we took one 5 cm diameter core of sediments to a depth of 10 cm from each of the 9 sampling positions along our marked transect to estimate grain size distributions and organic content. All sediment samples were frozen prior to analysis. After thawing, sediment samples were reduced to 40 to 80 g by coning and quartering (Ingram, 1971), and repeatedly washed with distilled water until salt-free, as tested by AgNO_3 . Samples then were dispersed with a Calgon solution and wet-sieved through a 62.5 μm mesh to separate the silt-clay fraction from coarser material. Silts were separated from clays by pipetting (Folk, 1974). All coarser material ($> 62.5 \mu\text{m}$) was dried at 90 °C, and sieved through US Standard sieves at 1 ϕ intervals for 10 min using a Ro-tap mechanical shaker (Ingram, 1971). All size fractions were weighed to the nearest 1 mg. To estimate percent organic carbon, one 1 g aliquot was taken from each sample before washing, passed through a 1 mm sieve to remove large particles, including macrobenthic animals, and dried to constant weight in a crucible at 105 °C. Then each aliquot was ashed at 550 °C for 4 h and reweighed, with weight loss used to estimate organic carbon (Gross, 1971).

Caging experiments

To test whether the effect of predation by large ($> 6 \text{ mm}$) epibenthic predators upon macrobenthic communities differed in unvegetated sediments and in the seagrass bed, we erected cages in both habitats. These cages were made of 6 mm mesh (black VEXAR plastic), attached by plastic-coated copper wire to 50 cm long steel rods at each corner. Each (square) cage covered an area of 1600 cm^2 . Cage walls and tops were sewn together with treated marine twine. The walls of the cages extended downwards 10 cm into the sediment and upwards to a 20 cm height on the sand

flat and to a 30 cm height in the seagrass bed (to permit full extension of seagrass blades).

Because many benthic species are themselves predatory (Ambrose, 1982) and because many epibenthic predators (largely decapod crustaceans) are small and mobile, a mesh cage, no matter how fine, will always fail to exclude all predators (e.g. Nelson, 1981; Virnstein et al., 1983). We were interested in excluding only the larger, mobile, epibenthic predators, which have been shown to be important in Chesapeake Bay (Virnstein, 1977) and which in the North Sea are equally well excluded by 1, 2, or 5 mm mesh, while unaffected by 20 mm mesh (Reise, 1978). We chose a mesh at the high end of the probable effective size range because the risks of reducing current flow, increasing organic deposition, and trapping invertebrate larvae all increase with declining pore sizes, as illustrated by the effects of 0.5 mm mesh cages in Reise's (1978) study. While this choice of mesh size restricts our exclusion to large ($> 6 \text{ mm}$) predators, we used identical mesh sizes and procedures in both habitats to permit our desired test of whether this size class of large predator has differential impact on the benthos in the 2 habitats.

We also installed partial cages, which were designed to reproduce most or all of the artificial effects of the caging while allowing predators normal access to the benthos. Partial cages were constructed to be exactly the same as complete cages except that they lacked the north wall (thereby continuing to cast a degree of shading similar to that under a full cage). Large predators (crabs, fishes, shrimps) utilized these partially-caged areas, although we have no measure of whether their abundance was similar in uncaged areas.

Three replicate full cages, partial cages, and undisturbed controls were positioned at each of 4 locations along a transect parallel to the sampling transect marked by the fixed stakes: sets of treatments were positioned 8 m within the seagrass bed and at 2, 4 and 8 m outside the seagrass bed. Different positions were used in the sand flat to permit a test of the hypothesis that the impact of predation on the sand-flat macrobenthos changed with distance from the nearest seagrass bed.

All cages were installed on 25 May 1977. On 25 July 1977, each cage was carefully inspected for evidence of any large predators. The one exclusion cage which did contain a 6 cm blue crab was not included in the results. The seagrass plants inside the complete and partial cages appeared green and healthy even after 2 mo of partial shading. After inspection of the cage interior, each exclusion cage and partial cage was carefully lifted out of the substratum. Upon removal of the caging, 2 core samples were immediately taken

from each previously-caged, partially-caged, and control area. The same methods were used in sampling this caging experiment as in the benthic sampling along the transect.

On 25 July 1977, the entire caging experiment was reestablished at nearby locations using the same cages and design as before. This second experiment ran for the same length of time, 2 mo, and was sampled in the identical way on 25 September 1977. Fouling of plastic surfaces required that cages be cleaned with a wire brush at least every third week during the course of both experiments. At this same frequency, drift algae (if present) were removed from inside partial cages. This entire caging experiment, including both time periods, produced 144 core samples: 2 dates (May-July and July-September), with 4 locations at each date (-8, 2, 4, 8 m), 3 treatments at each location (full cage, partial cage, and uncaged control), 3 replicate cages or areas (controls) per treatment, and 2 replicate cores (subsamples) per cage or area.

Sampling of epibenthic predators

To test whether abundances of large, epibenthic predators differed between inside and outside of the seagrass bed, we seined 10 m distances with a 3 m wide seine made of 6.3 mm nylon mesh (chosen to match the mesh size of our cages). Three such replicate hauls were made on each seining date at each of 3 locations: at the seagrass-bed boundary and at 15 m to either side of it. Seine hauls were made during the day on 17 June, 20 July, 3 September, 16 October, 19 November, and 15 December 1977. In addition, to test whether the daytime patterns in predator distribution remained similar at night, nocturnal seine samples were taken at 2300, 0330, and 0600 h (dawn) on 1 to 2 September 1977 and on 28 to 29 August and 1 to 2 September 1979. All animals caught in each seine haul were preserved in a buffered formalin solution and later identified to species and counted.

RESULTS

Benthic sampling along the fixed transect

On no occasion during the 6 mo of sampling was any macrophytic vegetation (either above- or below-ground) found in the sand flat, whereas the dry weight biomass of seagrasses (including epiphytes, roots, and rhizomes) was substantial in the seagrass bed (Fig. 1). The sampling location at the margin of the bed (0 m) produced consistently intermediate amounts of seagrass. A 2-way, mixed model ANOVA without replica-

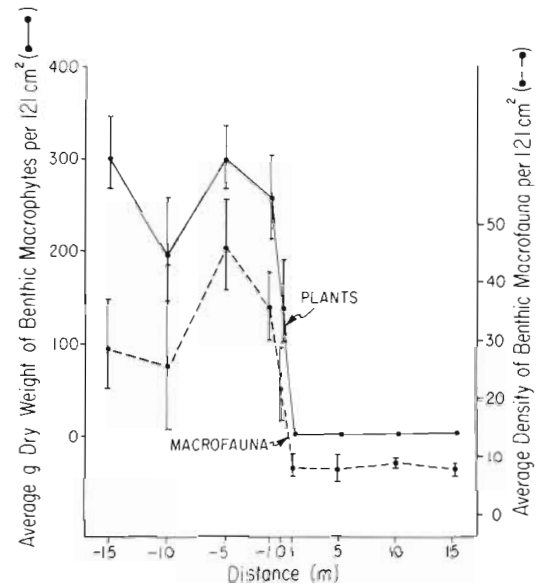


Fig. 1. Average g dry wt (± 1 SE) of all macrophytic plant material (solid line) and average density (± 1 SE) of all macrobenthos (dashed line) per core sample at each of 9 locations along a transect extending from 15 m inside a seagrass bed to 15 m out onto an adjacent sand flat. Data used to calculate each mean come from six 121 cm² \times 25 cm deep cores, taken at about 1 mo intervals at each location from 2 June through 17 December 1977. Negative distances represent distances into the seagrass bed

tion (with location as fixed factor and date as random factor) done on $\log_{10}(x + 1)$ -transformed dry weights showed no significant date effect. However, the location effect was highly significant ($p < 0.001$), with a preplanned Scheffé contrast showing average seagrass dry weights to be significantly higher ($p < 0.01$) inside the seagrass bed than on the sand flat. Although lack of replication prohibited testing for date-location interactions, t-tests done for each separate date revealed that the average $\log_{10}(x + 1)$ -transformed dry weight of seagrasses was always significantly (at least at $p < 0.025$) greater for the 4 seagrass locations than for the 4 sand-flat locations.

The average density of the macrobenthos along our transect followed directly the spatial distribution of seagrass biomass (Fig. 1). A 2-way, mixed model ANOVA without replication (with location as fixed factor and date as random factor) done on $\log_{10}(x + 1)$ -transformed macrofaunal densities revealed a significant ($p < 0.001$) location effect. A preplanned Scheffé contrast showed that the average macrobenthic density in the 4 seagrass positions was significantly ($p < 0.001$) greater than the average of the 4 sand-flat positions. In this analysis, there was also a significant ($p < 0.05$) date effect, with relatively low densities of macrobenthos in both July and October ($p < 0.05$ in 2 *a posteriori* Scheffé contrasts). This temporal pattern with multiple

non-consecutive minima in density suggests that there was no significant problem with potential autocorrelation. However, even if density data on successive months were not totally independent, the 2-way ANOVA still provides a conservative test of the location effect, which is the only one of direct relevance to our hypothesis.

To test the implicit assumption in an unreplicated 2-way ANOVA that there was no significant date-location interaction to confound interpretation of main effects, we grouped the data in 2 different ways and repeated the 2-way ANOVA, with replication within groups. We first grouped by consecutive trios of dates (replication of 3) and then repeated the analysis after grouping by trios of adjacent positions (replication of 3). Results were consistent, independent of way of grouping, in demonstrating no significant interaction effect. An additional 2-way, mixed model ANOVA, done on ungrouped (unreplicated), $\log_{10}(x + 1)$ -transformed sand-flat densities alone, revealed no significant location effect on macrobenthic density within the sand flat.

To improve our understanding of the relationship between the abundance of macrobenthos and the presence of seagrass, we separated the macrobenthos into groups based upon living position and trophic habits. We first separated (1) the epifauna adhering to the substrate or seagrass surface, (2) the mobile epibenthos, and (3) the infauna. Although the mobility criterion used to assign species to the proper epibenthic category (no. 1 or 2) was somewhat subjective, we made this separation because we suspected that the more motile species may react to the presence of cages and partial cages. We further subdivided the infauna into separate 'guilds' (*sensu* Root, 1967) of ecologically similar species: (1) predator-scavengers, (2) suspension feeders (most of which are in the surface sediments), (3) surface-deposit feeders, and (4) subsurface-deposit feeders (which feed below the sediment surface). Guild assignments were based upon information in Day (1967), Stanley (1970), Bloom et al. (1972), Bousfield (1973), Fauchald and Jumars (1979), Nelson (1979), Stoner (1980), and our own observations.

An unpublished appendix is available from the authors listing the most abundant species in each grouping, their relative abundances in both the seagrass bed and sand flat over the 6 mo sampling period, and their relative abundances in each treatment of the caging experiment. The epifauna was dominated by the gastropods *Bittium varium* and *Crepidula fornicata*, and the amphipods *Cymadusa compta* and *Melita appendiculata*. The mobile epibenthos was largely composed of the crustaceans *Hippolyte* spp. (*pleuracantha* and *zostericola* combined), xanthid crabs, and *Callinectes sapidus*, the bay scallop

Argopecten irradians, and the ophiuroid *Ophioderma brevispinum*. Nemerteans, *Nereis* spp. (*succinea* and *falsa* combined), *Glycera americana*, and the arabellid polychaete *Drilonereis magna* dominated the infaunal predator-scavengers. The spionid polychaetes *Prionospio heterobranchia* and *Streblospio benedicti*, the bivalve *Tagelus divisus*, *Sabella microphthalma*, and several ampeliscid amphipod species were the most numerous infaunal suspension feeders. The infaunal surface-deposit feeders were dominated by 3 bivalves *Tellina probina*, *T. versicolor*, and *Abra aequalis*, the isopod *Cyathura polita*, the gastropod *Acteocina canaliculata*, and the cirratulid polychaete *Tharyx marioni*. Infaunal subsurface-deposit feeders were dominated by polychaetes: the paraonid *Aricidea fragilis*, the maldanid *Axiothella mucosa*, and the capitellid *Notomastus hemipodus*.

Results of 2-way, mixed model ANOVA's on the $\log_{10}(x + 1)$ -transformed densities of each separate benthic group appear in Table 1. Because these tests of the effect of date and transect location were identical to the ones done on total macrobenthic density (also in Table 1), analogous reanalyses of group data were carried out to test the necessary assumption that date-location interactions were non-significant. For no group was the interaction effect significant in either ANOVA's grouping by dates or ANOVA's grouping by locations. Thus, the main effects in Table 1 can be interpreted without suspicion of confounding with date-location interactions.

Density varied significantly with date over our 6 mo sampling period for 6 of the 7 benthic groups (Table 1). The effect of position along the transect was significant for all groups except surface- and subsurface-deposit feeders. Each significant location effect was a consequence of the change from unvegetated to vegetated substrate: preplanned Scheffé contrasts showed the average density within the 4 seagrass-bed positions to be significantly (Table 1) greater than the average density of the 4 sand-flat positions for each group with a significant location effect. Furthermore, separate 2-way, mixed model ANOVA's performed on the 4 sand-flat sites alone and on the 4 seagrass-bed sites alone demonstrated no significant location effect for any group within either habitat type.

Because within-habitat effects were lacking, we pooled samples for all 4 locations within each habitat (Table 1) to permit a quantitative comparison of the effect of seagrass cover on each separate benthic group. Although the response of the 2 above-surface categories (epifauna and mobile epibenthos) to the presence of seagrasses was far stronger (52 ×) and significant at $\alpha = 0.001$ in preplanned Scheffé contrasts, the total infauna also showed nearly 3-fold higher densities inside the seagrass bed ($p < 0.01$ in a

Scheffé preplanned contrast). Within the infauna, the suspension-feeder guild exhibited the greatest proportionate response (a $4.2 \times$ increase) to the presence of the seagrasses, whereas the surface- and subsurface-deposit feeders showed a small and non-significant location effect in the ANOVA's (Table 1).

Species diversity indices calculated for each sample from the seagrass bed and from the sand flat demon-

strate some apparent differences between the two habitats (Table 2). Both for all the macrobenthos and for the infauna alone, median sample species diversity (H') and species richness (S) were lower in the sand flat ($p < 0.01$ in Wilcoxon 2-sample rank tests). However, this between-habitat difference appears to be entirely a consequence of a density bias: when diversity indices (Table 2, Rows c and f) were recalculated on the

Table 1. Analyses of effects of sampling date and location along the transect on the densities of all macrobenthic invertebrates and of several subsets of the macrobenthos. Samples were taken monthly from June to December 1977 at 9 locations along a transect extending from 15 m inside a seagrass bed to 15 m out onto an adjacent sand flat. The numerical densities in the seagrass bed and in the sand flat are presented for each benthic grouping (averaged over all 6 dates and 4 locations: $n = 24$); the ratios of those average densities appear in the final column

	Significance levels ^a in 2-way ANOVA's			Average density per 121 cm ² in seagrass (A)	Average density per 121 cm ² in sand flat (B)	Ratio ^c of A/B
	Date effect	Location effect	Date-location interaction ^b			
Total benthic invertebrates	*	***	NS, NS	39.0	8.7	4.5***
Total infauna	**	**	NS, NS	23.3	8.4	2.8**
Predator-scavengers	NS	***	NS, NS	7.0	1.9	3.7*
Suspension feeders	***	*	NS, NS	9.2	2.2	4.2*
Surface-deposit feeders	**	NS	NS, NS	2.9	1.9	1.5
Subsurface-deposit feeders	*	NS	NS, NS	3.3	2.0	1.7
Total mobile epibenthos	**	***	NS, NS	3.7	0.1	37.0***
Total epifauna	*	***	NS, NS	11.9	0.2	59.5***

(a) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS $p > 0.05$
(b) Date and location effects come from 2-way ANOVA without replication. Interaction effects come from 2 additional 2-way ANOVA's in which first dates and then locations were grouped by threes to provide replication and tests of interaction effects
(c) Significance of deviation from unity was determined by preplanned Scheffé contrasts between the 4 within-bed and 4 outside-bed locations. This contrast was performed only when location effect was significant ($p < 0.05$) in the 2-way ANOVA

Table 2. Average density, species diversity, species richness and species evenness per core sample from seagrass bed and sand flat. Averages are calculated from four 121 cm² samples taken on each of 6 dates from June to December 1977. Indices are calculated for total macrobenthic fauna and for infauna alone. In each case, an additional average is calculated for sand-flat data pooling 3 (at 5, 10, 15 m) or all 4 of the 4 individual samples on each date to remove the bias caused by density differences between seagrass-bed and sand-flat samples

Samples	Average density of fauna per sample	Average species diversity (H') per sample	Average species richness (S) per sample	Average species evenness (J') per sample
All samples of all benthic invertebrates				
(a) Seagrass bed	39.04	2.44	18.46	0.88
(b) Sand flat	8.71	1.76	6.67	0.96
Larger sand-flat samples formed by pooling all 4 individual samples (c)	34.65	2.66	18.00	0.93
All samples of infauna only				
(d) Seagrass bed	23.29	2.21	12.71	0.93
(e) Sand flat	8.38	1.72	6.42	0.96
Larger sand-flat samples of infauna only formed by pooling 3 of the individual samples (f)	24.67	2.44	13.50	0.94

H' = Shannon-Wiener information index = $-\sum p_i \ln p_i$; where p_i = relative abundance of the i^{th} species; S = total number of species; J' = Pielou's (1969) evenness = $H'/\ln S$

pooled totals of adjacent samples in the sand-flat habitat to remove the density bias, all apparent between-habitat differences disappeared. Wilcoxon 2-sample rank tests confirmed that no significant differences existed between habitats in any diversity index after pooling of sand-flat samples removed the large effect of differing density.

Sediment cores

Analyses of grain size distributions in cores taken at each sampling position along the permanent transect extending from 15 m into the sand flat to 15 m into the seagrass bed revealed differences between the 2 habitats. Fine sands (0.125 to 0.250 mm) dominated all sand-flat locations at a level of about 60 to 65 % by weight. Very fine sands (0.062 to 0.125 mm) contributed another 25 to 30 %. The seagrass-bed sediments were finer, with fine sand and very fine sand contributing approximately equally at about 40 to 45 % by weight. Silts and clays increased from an average of 3.2 % in the sand flat to an average of 11.3 % in the seagrass bed. Because of the generally finer sediments in the seagrass localities, the average graphic mean was significantly ($p < 0.01$ in a t-test) higher: 3.02 ϕ versus 2.85 ϕ in the sand flat. Organic carbon also was more abundant in the seagrass-bed sediments, although the difference was slight (1.3 % compared to 0.9 % by weight).

Caging experiments

To test the effect of caging treatment (exclusion vs partial caging vs uncaged controls) at the single seagrass position (-8 m), we subdivided the macrobenthos and for each of the 2 experiments ran separate 1-way, model I ANOVA's on the $\log_{10}(x + 1)$ -transformed mean densities (averaged over the 2 subsamples) of each benthic grouping. Bartlett's test demonstrated both the necessity and sufficiency of transformation to homogenize variances for each group in each date's experiment. In both the May-July and July-September experiments, the only group that showed a statistically significant response to caging treatment was the mobile epibenthos (Table 3). Two preplanned Scheffé contrasts revealed that this effect was a consequence of significantly ($p < 0.05$) higher densities in the partial cages than in the uncaged controls; partial cages and exclusion cages did not differ significantly. Our failure to demonstrate statistical significance in this comparison of partial cages and exclusion cages is partly a consequence of the power of the test: densities of mobile epibenthos were consistently 60 % higher

inside full cages than in partial cages in both experiments (Table 3). Similarly, there may be effects of caging on some infaunal guilds which our tests were not powerful enough to demonstrate. For instance, the density of the total infauna was consistently higher in full cages than in partial cages (by 13 % in the May-July experiment and 33 % in the July-September experiment) (Table 3). However, these effects are relatively small and permit the conclusion that caging had little effect on infaunal densities inside the seagrass bed and only some effect besides cage artifact on the above-ground benthos.

Caging had substantial effects on benthic abundances on the sand flat. Bartlett's tests showed a $\log_{10}(x + 1)$ transformation to be adequate to homogenize variances of each benthic group for each date's experiment. Separate 2-way, model I ANOVA's, done on the transformed mean densities (averaged over the 2 subsamples) of each benthic group to test the influence of caging treatment, experimental location (2, 4, or 8 m outside the seagrass bed), and their interaction, revealed general consistency of results across the 2 time periods (Table 4). Interaction effects were not significant in any of the 14 ANOVA's. The location effect was rarely significant, although there was a consistent location effect on the density of subsurface-deposit feeders. The caging effect was large and statistically significant in all but 1 analysis; in 7 analyses, the significance level was at $p < 0.001$ (Table 4). Infaunal densities inside exclusion cages were about 200 % higher than in controls and partial cages (Table 4), reaching levels indistinguishable (in t-tests using mean square errors from the ANOVA's) from those found in all 3 caging treatments in the vegetated community (Table 3) by the end of each experiment.

Results of ANOVA's and the 2 preplanned Scheffé contrasts (between controls and partial cages and between partial cages and exclusion cages) demonstrated 4 different types of response to caging (Table 4). For both above-ground benthic groups (epifauna and mobile epibenthos), Scheffé contrasts revealed that the cause of caging significance in both time periods was a significant difference between partial cages and uncaged controls, implying the existence of a cage artifact. The second type of response occurred consistently in both time periods for total infauna, predator-scavengers, and surface-deposit feeders. Scheffé contrasts for each of these groups (Table 4) consistently revealed the absence of cage artifacts (controls and partial cages did not differ) and the presence of significant effects of large predator exclusion (partial cages and exclusion cages differed). Suspension feeders revealed a third pattern of response in which for each time period both Scheffé contrasts were significant (Table 4), implying that cag-

Table 3. Effects of caging (uncaged controls, partial cages, and full exclusion cages) on the densities of various groupings of the macrobenthic fauna from 2 separate, successive 2 mo experiments in a seagrass bed; n = number of replicate cages or control plots

Benthic group	Average density ^a per 121 cm ²						Statistical significance of caging treatment from 1-way ANOVA's ^b	
	May-Jul			Jul-Sep			May-Jul	Jul-Sep
	Controls (n = 3)	Partial cages (n = 3)	Full cages (n = 3)	Controls (n = 3)	Partial cages (n = 3)	Full cages (n = 2)		
Total infauna	<u>41.7</u>	<u>46.2</u>	<u>52.7</u>	<u>18.3</u>	<u>22.7</u>	<u>30.5</u>	NS	NS
Predator-scavengers	<u>10.2</u>	<u>10.0</u>	<u>14.8</u>	<u>8.3</u>	<u>7.7</u>	<u>13.5</u>	NS	NS
Suspension feeders	<u>10.5</u>	<u>15.0</u>	<u>14.1</u>	<u>2.5</u>	<u>4.8</u>	<u>5.8</u>	NS	NS
Surface-deposit feeders	<u>3.0</u>	<u>8.0</u>	<u>7.3</u>	<u>3.3</u>	<u>7.3</u>	<u>6.0</u>	NS	NS
Subsurface-deposit feeders	<u>17.0</u>	<u>11.7</u>	<u>15.5</u>	<u>3.8</u>	<u>2.8</u>	<u>5.3</u>	NS	NS
Total mobile epibenthos	<u>1.3</u>	<u>8.2</u>	<u>13.2</u>	<u>2.3</u>	<u>25.2</u>	<u>43.0</u>	.	.
Total epifauna	<u>8.6</u>	<u>11.8</u>	<u>9.5</u>	<u>7.6</u>	<u>69.3</u>	<u>13.8</u>	NS	NS

(a) Underlining connects means that are not significantly different ($\alpha = 0.05$) in 2 Scheffé preplanned contrasts: (1) controls vs partial cages and (2) partial cages vs full cages. These contrasts were calculated only where ANOVA showed a significant caging effect. Where caging effect was non-significant, all means are connected by underlining
(b) * $p < 0.05$, NS $p > 0.05$

Table 4. Effects of caging (uncaged controls, partial cages, and full exclusion cages), location (2, 4, and 8 m away from seagrass-bed border), and their interaction on the densities of various groupings of the macrobenthic fauna from 2 separate, successive experiments on a sand flat; n = number of replicate cages or control plots

Benthic group	Average density ^a per 121 cm ²			Significance levels ^b in 2-way ANOVA's		
	Controls	Partial cages	Full cages	Caging effect	Location effect	Interaction effect
(A) May-Jul experiment	n = 9	n = 8	n = 9			
Total infauna	<u>11.1</u>	<u>15.1</u>	45.6	***	NS	NS
Predator-scavengers	<u>2.8</u>	<u>2.7</u>	9.1	***	**	NS
Suspension feeders	2.5	6.2	22.1	***	NS	NS
Surface-deposit feeders	<u>1.9</u>	<u>2.7</u>	7.8	***	NS	NS
Subsurface-deposit feeders	<u>2.8</u>	<u>2.5</u>	5.3	**	***	NS
Total mobile epibenthos	0.3	<u>4.4</u>	<u>1.9</u>	**	NS	NS
Total epifauna	0.2	<u>2.1</u>	<u>1.1</u>	**	NS	NS
(B) Jul-Sep experiment	n = 9	n = 9	n = 9			
Total infauna	<u>9.3</u>	<u>10.9</u>	29.9	**	NS	NS
Predator-scavengers	<u>2.3</u>	<u>2.5</u>	8.2	***	NS	NS
Suspension feeders	1.3	2.3	8.6	***	NS	NS
Surface-deposit feeders	<u>3.2</u>	<u>3.0</u>	9.1	.	NS	NS
Subsurface-deposit feeders	<u>2.2</u>	<u>3.1</u>	<u>3.6</u>	NS	.	NS
Total mobile epibenthos	0.6	<u>2.8</u>	<u>3.7</u>	***	NS	NS
Total epifauna	0.6	2.1	0.9	.	NS	NS

(a) Underlining connects means that are not significantly different ($\alpha = 0.05$) in 2 Scheffé preplanned contrasts: (1) controls vs partial cages and (2) partial cages vs full cages. These contrasts were calculated only where ANOVA showed a significant caging effect. Where caging effect was non-significant, all means are connected by underlining
(b) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS $p > 0.05$

ing artifacts contributed along with predation in creating the significant caging effect indicated by the ANOVA's. Subsurface-deposit feeders also showed a unique response to caging: in the first experiment, this

guild exhibited a significant, but small, effect of predator exclusion with no cage artifact, whereas ANOVA revealed that the caging treatment was non-significant in the second experiment.

Calculation of average sample diversity indices for each of the caging treatments (Table 5) demonstrated differences between the sand-flat and seagrass-bed experiments. In the seagrass bed, Wilcoxon 2-sample rank tests showed no significant differences between controls and partial cages or between partial cages and full cages in species diversity (H'), species richness (S), or species evenness (J'). In addition, the caging experi-

ment produced no significant effect on any index calculated on the infauna alone for either experimental period (results not shown). In the sand-flat habitat, there were some significant differences in sample species diversity between caging treatments (Table 5). However, all differences disappeared after samples from controls and partial cages were pooled by pairs and the indices recalculated on the larger samples to

Table 5. Average total benthic density, species diversity (H'), species richness (S), and species evenness (J') per core sample from caging experiments in the seagrass bed and sand flat. Averages are calculated from 18 cores (2 per cage for 9 replicate cages) for each treatment in the sand flat and from 6 cores (2 per cage for 3 replicate cages) for each treatment in the seagrass bed. In the final 2 rows, both control and partial cage samples are pooled by pairs to provide a test of the influence of density differences on diversity indices in the sand-flat experiment^a

Treatment	Average faunal density ^b		Average species diversity (H')		Average species richness (S)		Average species evenness (J')	
	May-Jul	Jul-Sep	May-Jul	Jul-Sep	May-Jul	Jul-Sep	May-Jul	Jul-Sep
Seagrass-bed experiments								
(A) Controls	56.6	29.0	2.41	2.40	21.0	15.8	0.81	0.91
(B) Partial cages	66.3	120.7	2.91	2.35	26.7	21.7	0.89	0.81
(C) Full cages	78.0	87.3	2.93	2.41	29.8	25.0	0.86	0.76
Sand-flat experiments								
(D) Controls	11.6	10.6	1.96*	1.82*	8.2**	7.8**	0.96	0.96
(E) Partial cages	21.7	15.8	2.28	2.11	13.3	10.6	0.94	0.94
(F) Full cages	46.8	34.6	2.25	2.56	20.1**	17.7**	0.85	0.92
Sand-flat experiments where control and partial cage samples are pooled by pairs								
(G) Controls	23.1	21.3	2.45	2.44	13.7	14.4	0.95	0.96
(H) Partial cages	43.4	31.7	2.79	2.63	22.2	17.9	0.92	0.93

(a) Significance of differences tested by Wilcoxon 2-sample rank tests, first comparing controls with partial cages and then partial cages with full cages. * $p < 0.05$, ** $p < 0.01$, no notation $p > 0.05$

(b) Slight discrepancies occur between averages given here and in Table 4, because here all cores were averaged without weighting, whereas in Table 4 an average value was first calculated for each cage or control plot before calculating a grand mean. Where any core was lost, these 2 methods produce slightly different results

Table 6. Catch from seine hauls in the vicinity of benthic transects and caging experiments. Daytime seine hauls represent total catch from 18 hauls (3 m wide \times 10 m long) taken as 3 parallel replicates on each of 6 dates from June to December 1977. Night-to-dawn hauls represent for each time the total catch from 9 hauls (3 m \times 10 m) taken as 3 parallel replicates on each of 3 dates in late August and early September. Only large (> 6 mm) potential benthic feeders are listed, but inclusion of the rarer *Opsanus tau* and *Mycteroperca microlepis* would not alter general patterns

Species	Daytime seine hauls			Night-to-dawn seine hauls								
	Sea-grass bed	Edge	Sand flat	2300 h			0300 h			dawn 0600 h		
				Sea-grass bed	Edge	Sand flat	Sea-grass bed	Edge	Sand flat	Sea-grass bed	Edge	Sand flat
<i>Lagodon rhomboides</i>	114	47	0	63	34	58	74	43	3	9	17	2
<i>Penaeus</i> spp. (<i>aztecus</i> and <i>duorarum</i>)	9	13	0	190	158	68	150	58	30	29	14	0
<i>Callinectes sapidus</i>	10	9	0	29	19	5	24	13	4	55	5	0
<i>Monacanthus hispidus</i>	9	2	0	5	2	0	1	0	0	2	1	0
<i>Leiostomus xanthurus</i>	2	5	0	0	0	0	0	0	0	0	0	0
<i>Orthopristis chrysoptera</i>	1	1	0	8	6	7	13	1	2	1	1	0
<i>Libinia dubia</i>	1	1	0	0	0	0	0	0	0	0	1	0
<i>Bairdiella chrysoura</i>	0	0	0	0	2	0	3	4	1	0	3	0
Total potential benthic predators	146	78	0	295	221	138	265	119	40	96	42	2

remove sample-size (density) differences between treatments. A similar pattern (results not shown) of significance which was also removed by approximate equalization of densities appeared in diversity indices calculated on the infauna alone from the sand-flat caging experiment. It thus appears that the only effect of caging treatments on sample species diversity indices was an indirect consequence of the creation of density differences.

Seining for epibenthic predators

Daytime seining collected substantial numbers (Table 6) of a variety of species known to prey upon benthos to some degree in local sounds (Adams, 1976). Ranked by abundance in our samples, this group was comprised of pinfish *Lagodon rhomboides*, penaeid shrimps *Penaeus aztecus* and *P. duorarum*, blue crabs *Callinectes sapidus*, file fish *Monacanthus hispidus*, spot *Leiostomus xanthurus*, pig fish *Orthopristis chrysoptera*, and spider crabs *Libinia dubia*. Also captured, but not included in our analyses, were planktivores, such as the bay anchovy *Anchoa mitchelli*, and higher-order carnivores, such as the toad fish *Opsanus tau* and the gag grouper *Mycteroperca microlepis*. Other small benthic predators do exist in this system (many are included under mobile epibenthos in the appendix), but we designed our seining to capture those same species excluded by the 6 mm mesh used in our caging experiment.

Table 6 lists the patterns of abundance of benthic predators collected in daytime seine hauls. Not a single capture was recorded from sand-flat seining. Most individuals came from seagrass-bed hauls, while seining along the margin of the 2 habitats produced intermediate numbers. A 2-way, mixed model ANOVA was performed on $\log_{10}(x + 1)$ -transformed catch data from each of the 6 daytime dates for each predator species and for groups of species to test whether location (inside vs outside vs edge of seagrass bed) and/or date had any significant effect on catch totals. ANOVA's revealed that the location effect (densities highest in seagrass and lowest on the sand flat) was significant for *Callinectes sapidus* and *Penaeus* spp. at $p < 0.05$, and for both benthic feeding fishes combined and all benthic predators combined (the sum of the 3 categories) at $p < 0.001$. Temporal differences were significant only for the benthic-feeding fishes and the total of all categories: fish densities in November and December were lower than in the warmer months ($p < 0.05$ in an *a posteriori* Scheffé contrast).

Except for the addition of the silver perch *Bairdiella chrysoura*, the nocturnal seining produced the same group of benthic-feeding predators (Table 6). We

pooled the results from all dates in Table 6 to illustrate the 2 major patterns in these data. First, the total number of benthic-feeding predators per seine haul was greater ($p < 0.01$ in a χ^2 test) at night (2300 and 0300 h) than during daylight (0600 h). Second, although the daytime pattern of greater predator abundance inside the seagrass bed usually persisted at night, the contrast between habitats was not nearly so great ($p < 0.01$ in a $3 \times 3 \chi^2$ contingency test): benthic-feeding predators were captured on the sand flat in large numbers at night.

DISCUSSION

In Back Sound, North Carolina, macrobenthic abundances were significantly greater inside a seagrass bed than on the adjoining sand flat, as found in other temperate and subtropical localities (e.g. Kikuchi, 1966; O'Gower and Wacasey, 1967; Warme, 1971; Santos and Simon, 1974; Thayer et al., 1975; Orth, 1977; Reise, 1977; Brook, 1978; Stoner, 1980; Peterson, 1982; Virnstein et al., 1983). The higher densities inside the seagrass bed were not solely due to epibenthic groups of species, which may require the actual presence of seagrass blades or macroalgae for suitable habitat and/or substratum. The infauna also was significantly more dense within the seagrass bed, although the between-habitat density difference was smaller ($3 \times$) than that exhibited by the two epibenthic groups ($52 \times$).

The presence of this between-habitat pattern in infaunal densities made appropriate a test of Reise's (1977) hypothesis that differential rates of predation by epibenthic predators are largely responsible for higher infaunal densities in seagrass. The macrobenthic infauna in our seagrass bed exhibited a small and statistically non-significant response to exclusion of large (> 6 mm) epibenthic predators, whereas the infauna on the adjacent sand flat increased substantially and significantly in the absence of large epibenthic predators. Within cages that excluded predators larger than 6 mm, infaunal densities in the sand flat rose to levels indistinguishable from those that occurred naturally in the seagrass bed. These results support the hypothesis that predation by large epibenthic consumers is not an important determinant of macro-infaunal density in temperate-zone seagrass beds but does reduce macro-infaunal densities on nearby unvegetated bottoms. Our study did not address the potential role of smaller (< 6 mm) predators, which may also have effects that vary with habitat (e.g. Nelson, 1981; Virnstein et al., 1983). Nevertheless, the presence of seagrasses appears to provide the macro-infauna some degree of natural refuge from large epibenthic predators.

The caging results were repeated with close fidelity in each of 2 successive experiments, one from May to July and the other from July to September. This implies that the between-habitat difference in predation pressure by large epibenthic consumers remained virtually constant over those 2 time periods. If this predation process is a major cause of the between-habitat difference in infaunal densities, then one would not expect the magnitude of the difference in infaunal densities between habitats to vary greatly over this 4 mo period. Our analyses of the sampling data from the transect extending from the sand flat into the seagrass bed confirmed that over the period of June to December the magnitude of the between-habitat difference in infaunal densities never changed (i.e. the date-location interaction was non-significant in all ANOVA's).

The differential-predation hypothesis gains further support from separating the infauna into separate guilds (analogous to Stoner, 1980) and demonstrating the similarity in the relative magnitudes of the response of each guild to the presence of seagrasses along the transect and in the response to caging on the sand flat. Suspension feeders responded the most to the presence of seagrass, predator-scavengers an intermediate amount, and the 2 deposit-feeding guilds the least. Essentially the same pattern in the relative and absolute responses of different infaunal guilds was reproduced by caging experiments in the sand flat. To illustrate the similarity in response of infauna to seagrass along the transect and in infaunal response to caging on the sand flat, we combined both data sets and normalized both responses relative to controls to permit comparisons (Table 7). The similarity in these 2 response patterns supports the hypothesis that heavy predation by large epibenthic consumers on the

infauna of unvegetated sediments is at least partly responsible for the macro-infaunal density difference between seagrass beds and nearby unvegetated bottoms.

Although a similar conclusion has been reached by other workers in different localities (Orth, 1977; Virnstein, 1977; Reise, 1977, 1978), previous studies have not convincingly controlled for caging artifacts. The 2 potential artifacts of greatest concern in studying the infauna are: (1) baffling effects caused by the cage structure slowing currents and causing deposition of both organic-rich fine sediments and invertebrate larvae (Hulberg and Oliver, 1980); (2) effects of increasing consumer densities inside partial cages and exclusion cages as small (often growing juvenile) predators seek refuge from their enemies (Young and Young, 1978; Nelson, 1981; Virnstein et al., 1983). To minimize the baffling artifact, we chose a relatively large mesh size (6 mm) for our cages and focused attention on the larger consumers. The second type of artifact does appear in our data. The mobile epibenthos, which includes several predatory species, was consistently more abundant under partial cages and full cages than in uncaged controls in both habitats.

To assess the importance of these artifacts in influencing our conclusions, one needs to compare actual faunal densities under partial cages to those in uncaged controls and in full cages. The partial cages were designed to reproduce most of the artifacts of caging but still allow access by the important large consumers. If cage artifacts seriously affected our conclusions in the seagrass, where infaunal densities were approximately equal under all 3 caging treatments, one would need to postulate the existence of an artifact that exactly compensated for an unseen effect of predator exclusion. For instance, compensatory predation

Table 7. Relative response of each infaunal guild to presence of seagrass along the transect compared to relative responses to caging on the sand flat. 1x = no increase. Caging responses are partitioned into artifact and response to predator exclusion, assuming that differences between partial cages and controls estimate the magnitude of cage artifacts and that differences between partial cages and full cages estimate the effect of predator exclusion (as demonstrated by Scheffé tests in Table 4). Parentheses enclose statistically non-significant ($p > 0.05$) responses (from Tables 1 and 4). Caging responses represent average responses over the 2 experiments

Infaunal guild	Response to seagrass	Average responses to caging in sand flat		
		Artifact	Predator exclusion	Total ^a
Suspension feeders	4.2 ×	2.1 ×	3.7 ×	7.7 ×
Predator-scavengers	3.7 ×	(1.4 ×)	3.6 ×	4.1 ×
Surface-deposit feeders	(1.5 ×)	(1.2 ×)	3.0 ×	3.2 ×
Subsurface-deposit feeders	(1.7 ×)	(1.1 ×)	(1.6 ×) ^b	(1.7 ×) ^b

(a) Total response confounds both artifact and effect of predator exclusion by multiplying the 2 (as in ANOVA results in Table 4)

(b) This response was significant on one date, but not the other

by the microconsumers (< 6 mm) could have obliterated an increase in infaunal density that occurred under full cages in the absence of large consumers. This is possible, but by Occam's razor, a more parsimonious conclusion is that predation by large epibenthic consumers plays a relatively minor role in determining infaunal densities in the seagrass bed.

Similarly, in the sand flat, where infaunal densities were highest under full cages and essentially identical in partial cages and uncaged controls, one would need to invoke the existence of a pair of exactly compensating artifacts to reject our conclusion that macrobenthic predation is an important determinant of infaunal density in that habitat. For instance, baffling could have increased infaunal densities under both full and partial cages, but the subsequent increases in abundance of macroconsumers inside partial cages (to which they had free access – the 'artificial reef' effect of Peterson, 1979) would need to have reduced the macro-infaunal densities by an exactly equal amount. This, too, is possible but our conclusion that macrobenthic predation is important in the sand flat is more parsimonious.

Although cage artifacts do not seem to confound our interpretation of the responses of the macro-infauna to caging, the epifauna and mobile epibenthos exhibited substantial cage artifacts in our experiments. The mechanisms probably included the provision of increased surface space (analogous to the presence of seagrass blades) provided by the cage as well as the provision of refuge from some large consumers. Scallops need a surface on which to settle and did settle heavily on our cage surfaces. Gastropods crawled on the inside and outside of the cages. Because of the extent of these artifacts, we draw no conclusions about the importance of predation on either epibenthic group.

The differing responses of the 4 infaunal guilds both to caging and to the presence of seagrass (Table 7) probably have ecological significance. Suspension feeders represent the only infaunal guild to show a significant cage artifact. The simultaneous influence of this artifact and a real effect of predator exclusion explains why the suspension feeders responded to caging on the sand flat far more than any other guild (Table 7). If this artifact of caging to which suspension feeders responded is an effect also created naturally by the presence of seagrass (e. g. current baffling by the projections into the water column), then the relatively large response of suspension feeders to the presence of seagrass may also be a consequence of the simultaneous action of two natural effects of seagrass: predator exclusion and a physically-mediated effect like current baffling.

The relatively large responses of the predator-

scavenger guild to the presence of seagrass and to the exclusion of large epibenthic predators from the sand flat (Table 7) may be explained by the trophic position of this group. These infaunal predators tend to be larger than the other infauna and, therefore, more likely to be preyed upon by epibenthic predators (Ambrose, 1982). In contrast, the surface- and subsurface-deposit feeders include many prey species for the infaunal predator-scavengers. Consequently, exclusion of epibenthic predators does not remove a major predator for many of these deposit-feeding species and, for some species in these guilds, predation rates may even be increased as the density of infaunal predator-scavengers increases (Young and Young, 1978; Virnstein, 1979). This process may explain why the 2 deposit-feeding guilds show relatively small responses to seagrass and to exclusion of epibenthic predators from the sand flat. Because increasing depth in the sediment helps protect infauna from predators (e. g. Woodin, 1978; Virnstein, 1979), the small and, on one occasion insignificant, response of the generally deeper-dwelling, subsurface-deposit feeders can be explained by their naturally limited susceptibility to predation.

Peterson (1979) reviewed all available caging studies in marine and estuarine soft sediments and concluded that there was no evidence in this system of declining species diversity and increasing dominance in the absence of large predators, as would be predicted from results of analogous experiments in the marine rocky intertidal zone. The patterns in average species richness, diversity, and evenness per sample in this study support and extend this conclusion. Although macrobenthic densities increased substantially under full cages in the sand-flat habitat, species diversity, richness, and evenness did not decline. Similarly, the increased macro-infaunal densities in the seagrass bed, which appears to serve as a partial natural predation refuge for infauna, were not accompanied by lower species diversity and increased dominance. By pooling replicate samples, we were able to demonstrate empirically that sample species diversity, richness, and evenness all increased with increasing local density in the fashion that would be predicted from a simple species-individuals curve. Thus, a null-hypothesis, non-interactive model (requiring no competition or interactive effects at all) was sufficient to explain all sample diversity differences between the two habitats and between caging treatments.

Although our conclusions about the differing importance of epibenthic predation in vegetated and unvegetated soft sediments are in general agreement with conclusions from previous studies (Virnstein, 1977; Orth, 1977; Reise, 1977, 1978; Nelson, 1979; Peterson, 1979, 1982; Heck and Thoman, 1981; Stoner, 1982), an

unresolved paradox still exists. While most researchers seem to agree that predation on infauna by large epibenthic consumers is more significant outside of seagrass beds, there is abundant evidence demonstrating that mobile epibenthic species (the faunal grouping that includes these predators) are more abundant, often by orders of magnitude, inside the seagrass habitat (Briggs and O'Connor, 1971; Heck and Wetstone, 1977; Heck and Orth, 1980; Orth and Heck, 1980). In many cases, such as in our daylight sampling, seining and trawling in unvegetated subtidal areas of the estuary produce almost no epibenthic predators. This pattern may be an artifact, in that the seine may be more visible and easily escaped during daylight in unvegetated areas. However, we detected no evident escape by fishes, crabs, and shrimps from ahead of our seine, suggesting that this artifact was not serious. If the pattern of predator absence from unvegetated areas during daylight is real, then one must pose the question of where and what are these predators, supposedly so important as to limit densities and diversities of benthos throughout the sand flat.

We propose a series of largely untested hypotheses to resolve this apparent paradox. Results of our night seining and of day and night trawling studies in Chesapeake Bay (Heck and Orth, 1980; Orth and Heck, 1980) demonstrated that at night epibenthic predators can be found in abundance on unvegetated flats. Heck and Wetstone (1977) argued that the mobile epibenthos as a group is virtually restricted to vegetated habitats or habitats with effective refugia as an adaptive response to avoiding their own predators. Because these higher-order predators (often larger fishes, see Orth and Heck, 1980) search by visual clues, the seagrass bed provides a partial refuge for their prey, the bulk of the mobile epibenthos (Randall, 1967). However, darkness can provide a similar refuge, and we suggest that those members of the mobile epibenthos that emerge from the seagrass beds to feed in the sand flat do so only at night because of the great risk of predation in daylight.

This refuge model is analogous to a variety of similar models of how physical refugia and structural heterogeneity function in the organization of biological communities. For example, small rodents foraging away from the protection of shrubs are thought to be responsible for the bare, grazed patches around chaparral plants (Bartholomew, 1970). In the marine environment, Ogden et al. (1973) have demonstrated that sea urchins take cover around coral heads during the day, but then graze down seagrasses in the coral's vicinity under the protection of darkness. Woodin (1978, 1981) demonstrated that the presence of physical structures such as worm tubes or soda straws (as abiotic analogues for worm tubes) inhibits the effectiveness of

predators and thereby permits the persistence of atypically high densities of benthic infauna in the immediate vicinity of a group of such tubes.

In each of these examples, including our own, the presence of a physical refuge from predation plays a significant role in community organization and has important implications. In those instances where predators inhabit the refuge and emerge only during times of relatively low risk, the rate of their feeding activity should decline with increased distance from the nearest suitable refuge. Although we failed to demonstrate variable effects of excluding predators as a function of distance from the seagrass bed, we used only a small range of distances. Over a broader range, appropriate to the foraging radius of the dominant benthic-feeding predators, we predict variations in infaunal abundances as a consequence of the varying rates of predation. A rigorous test of this prediction might provide a simultaneous test of our proposed model of predator-controlled benthic community organization in the vicinity of temperate seagrass beds.

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LITERATURE CITED

- Adams, S. M. (1976). Feeding ecology of eelgrass fish communities. *Trans. Am. Fish. Soc.* 105: 514-519
- Ambrose, W. G., Jr. (1982). The influence of the predatory polychaetes *Glycera dibranchiata* and *Nereis virens* on the structure of a soft-bottom community in a Maine estuary. Ph. D. thesis, University of North Carolina, Chapel Hill
- Bartholomew, B. (1970). Bare zone between California shrub and grassland communities: the role of animals. *Science*, N. Y. 170: 1210-1212
- Bloom, S. A., Simon, J. L., Hunter, V. D. (1972). Animal-sediment relations and community analysis of a Florida estuary. *Mar. Biol.* 13: 43-56
- Bousfield, E. L. (1973). Shallow water gammaridean amphipods of New England. Cornell University Press, Ithaca

- Briggs, P. T., O'Conner, J. S. (1971). Comparison of shore-zone fishes over naturally vegetated and sand-filled bottoms in Great South Bay. *Jl N. Y. Fish Game* 18: 15-41
- Brooks, I. M. (1978). Comparative macrofaunal abundance in turtlegrass (*Thalassia testudinum*) communities in south Florida characterized by high blade density. *Bull. mar. Sci.* 28: 212-217
- Day, J. H. (1967). A monograph on the Polychaeta of southern Africa. British Museum (Natural History), London, Publ. No. 656: 1-878
- Dayton, P. K., Oliver, J. S. (1980). An evaluation of experimental analyses of population and community patterns in benthic marine environments. In: Tenore, K. R., Coull, B. C. (ed.) *Marine benthic dynamics*. University of South Carolina Press, Columbia, p. 93-120
- Fauchald, K., Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. A. Rev.* 17: 193-284
- Folk, R. L. (1974). *Petrology of sedimentary rocks*. Hemphill Publishing Co., Austin
- Gross, M. G. (1971). Carbon determination. In: Carver, R. E. (ed.) *Procedures in sedimentary petrology*. Wiley-Interscience, New York, p. 573-596
- Heck, K. L., Jr., Orth, R. J. (1980). Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay-decapod Crustacea. *Estuaries* 3: 289-295
- Heck, K. L., Jr., Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habitats. *J. exp. mar. Biol. Ecol.* 53: 125-134
- Heck, K. L., Jr., Wetstone, G. S. (1977). Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *J. Biogeogr.* 4: 135-143
- Holland, A. F., Mountford, N. K., Hiegel, M. H., Kaumeyer, K. R., Mihursky, J. A. (1980). Influence of predation on infaunal abundance in Upper Chesapeake Bay, USA. *Mar. Biol.* 57: 221-235
- Hulberg, L. W., Oliver, J. S. (1980). Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. *Can. J. Fish. aquat. Sci.* 37: 1130-1139
- Ingram, R. L. (1971). Sieve analysis. In: Carver, R. E. (ed.) *Procedures in sedimentary petrology*. Wiley-Interscience, New York, p. 49-94
- Kikuchi, T. (1966). An ecological study on animal communities of the *Zostera marina* belt in Tomioka Bay, Amakusa, Kyushu. *Publ. Amakusa Mar. Biol. Lab.* 1: 1-106
- Nelson, W. G. (1979). An analysis of structural pattern in an eelgrass (*Zostera marina*) amphipod community. *J. exp. mar. Biol. Ecol.* 39: 231-264
- Nelson, W. G. (1981). The role of predation by decapod crustaceans in seagrass ecosystems. *Kieler Meeresforsch., Sonderh.* 5: 529-536
- Ogden, J. C., Brown, R. A., Saleska, N. (1973). Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science, N. Y.* 182: 715-717
- O'Gower, A. K., Wacasey, J. W. (1967). Animal communities associated with *Thalassia*, *Diplanthera*, and sand beds in Biscayne Bay. I. Analysis of communities in relation to water movements. *Bull. mar. Sci.* 17: 175-210
- Orth, R. J. (1977). The importance of sediment stability in seagrass communities. In: Coull, B. C. (ed.) *Ecology of marine benthos*. University of South Carolina Press, Columbia, p. 281-300
- Orth, R. J., Heck, K. L., Jr. (1980). Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay-fishes. *Estuaries* 3: 278-288
- Peterson, C. H. (1979). Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston, R. J. (ed.) *Ecological processes in coastal and marine systems*. Plenum Press, New York, p. 233-264
- Peterson, C. H. (1982). Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar. Biol.* 66: 159-170
- Pielou, E. C. (1969). *An introduction to mathematical ecology*. Wiley-Interscience, New York
- Randall, J. E. (1967). Food habits of the reef fish of the West Indies. *Proceedings of the International Conference on Tropical Oceans* 5: 665-847
- Reise, K. (1977). Predation pressure and community structure of an intertidal soft bottom fauna. In: Keegan, B. F., Ceidigh, P. O., Boaden, P. J. S. (ed.) *Biology of benthic organisms*. Pergamon Press, New York, p. 513-519
- Reise, K. (1978). Experiments on epibenthic predation in the Wadden Sea. *Helgoländer wiss. Meeresunters.* 31: 51-101
- Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* 37: 317-350
- Santos, S. L., Simon, J. L. (1974). Distribution and abundance of the polychaetous annelids in a south Florida estuary. *Bull. mar. Sci.* 24: 669-689
- Stanley, S. M. (1970). Relation of shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America Memoir* No. 125: 1-296
- Stoner, A. W. (1980). The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull. mar. Sci.* 30: 537-551
- Stoner, A. W. (1982). The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). *J. exp. mar. Biol. Ecol.* 58: 271-284
- Sutherland, J. P., Karlson, R. H. (1977). Development and stability of the fouling community at Beaufort, North Carolina. *Ecol. Monogr.* 47: 425-446
- Taylor, J. D., Lewis, M. S. (1970). The flora, fauna, and sediments of the marine grass beds of Mabe, Seychelles. *J. nat. Hist.* 4: 199-220
- Tegner, M. J., Dayton, P. K. (1981). Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Mar. Ecol. Prog. Ser.* 5: 255-268
- Thayer, G. W., Adams, S. M., LaCroix, M. W. (1975). Structural and functional aspects of a recently established *Zostera marina* community. In: Cronin, L. E. (ed.) *Estuarine research, Vol. 1, Chemistry, biology, and the estuarine system*. Academic Press, New York, p. 518-540
- Virnstain, R. W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58: 1199-1217
- Virnstain, R. W. (1978). Predator caging experiments in soft sediments: caution advised. In: Wiley, M. L. (ed.) *Estuarine interactions*. Academic Press, New York, p. 261-273
- Virnstain, R. W. (1979). Predation on estuarine infauna: response patterns of component species. *Estuaries* 2: 69-86
- Virnstain, R. W., Mikkelsen, P. S., Cairns, K. D., Capone, M. A. (1983). Seagrass beds versus sand bottoms: the trophic importance of their associated benthic invertebrates. *Fla Sci.* 45: 491-509
- Warme, J. E. (1971). Paleocological aspects of a modern coastal lagoon. *Univ. Calif. Publ. geol. Sci.* 87: 1-131
- Woodin, S. A. (1978). Refuges, disturbance, and community

-
- structure: a marine soft-bottom example. *Ecology* 59: 274-284
- Woodin, S. A. (1981). Disturbance and community structure in a shallow water sand flat. *Ecology* 62: 1052-1066
- Young, D. K., Buzas, M. A., Young, M. W. (1976). Species densities of macrobenthos associated with seagrass: a field experimental study of predation. *J. mar. Res.* 34: 577-592
- Young, D. K., Young, M. W. (1978). Regulation of species densities of seagrass-associated macrobenthos: evidence from field experiments in the Indian River estuary, Florida. *J. mar Res.* 36: 569-593

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