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Regulation of species densities of seagrass-associated macrobenthos: Evidence from field experiments in the Indian River estuary, Florida

by David K. Young[1] and Martha W. Young[2]

ABSTRACT

In order to provide insight into the regulation of species densities of seagrass-associated macrobenthos, field experiments in the Indian River estuary, Florida were initiated in the seagrass *Halodule wrightii* to test effects of (1) excluding predators by caging, (2) enclosing predators inside cages, (3) adding dense populations of suspension feeders, (4) providing organic enrichment, (5) removing seagrass blades, and (6) erecting cages at different times.

The 11 most abundant species were selected for statistical testing of responses to the experimental treatments. Analyses showed that macrobenthic species differed markedly in their responses to the various treatments over a period of one year. Several species had increased densities with organic enrichment and one increased depending on the time when a cage was erected. Some species had increased densities when seagrass blades were clipped while others showed decreased densities when blades were removed. Certain species occurred in high densities only inside predator exclusion cages. These variations in response did not consistently correspond to taxonomic groupings or feeding types.

These field experiments may encourage caution by marine ecologists wishing to generalize from one species or group of species to the community level of organization.

1. Introduction

Fostered by the pioneer work of Petersen (1918) in Danish waters, attention has

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focused on seagrasses as the foundation of one of the most productive shallow-water ecosystems in the sea (reviewed by McRoy and McMillan, 1977). Little is known of how seagrass production is translated through the food web to higher consumers. Since few species graze directly upon seagrasses, seagrass detritus, or more specifically, the microorganisms associated with seagrass decomposition, are considered the most important food source for detritivores in the seagrass-based food web (Fenchel, 1977; Tenore, 1977). In addition to their high primary productivity, seagrasses have been shown to provide physical refuge from predation for certain fishes and invertebrates (Carr and Adams, 1973; Kikuchi, 1974; Reise, 1977), to trap and stabilize sediment (Ginsburg and Lowenstam, 1958; Burrell and Schubel, 1977; Orth, 1977), and to furnish surface area for attached plants and animals (Humm, 1964; Nagle, 1968; Rasmussen, 1973).

It is not known how seagrasses provide their presumed support of commercially important fisheries. Contradictory views have been expressed by workers studying seagrasses in different parts of the world. For example, Rasmussen (1977) reported that the expected catastrophic impact upon Baltic and North Sea fisheries did not occur in the 1930's following the mass destruction of the seagrass *Zostera marina* by the "wasting disease." On the other hand, Kikuchi and Pérès (1977) presented evidence from the Seto Inland Sea of Japan that certain fish species of commercial importance suffered a decline coincident with drastic reductions in coverage by *Zostera marina* seagrass beds resulting from land filling and water pollution. As Steele (1974) has shown for other marine ecosystems, our present knowledge of the intermediate consumer levels of the seagrass-based food web is inadequate to resolve such apparent contradictions.

In order to provide additional insight into the structure and function of the seagrass-associated macrobenthos, experiments using predator exclusion cages were initiated in pure stands of the sea grass *Halodule* (=*Diplanthera*) *wrightii* Ascherson on the east central coast of Florida (Young *et al.*, 1976; Young and Young, 1977). These experiments revealed the importance of small opportunistic benthic species as prey, and of decapod crustacean predators as "translators" of energy from the macrobenthos to higher level consumers. Salinity, temperature, and tidal fluctuations were shown to be relatively unimportant in directly affecting macrobenthic community structure. The time when an experiment is begun was suggested as an important determinant of cage effects upon densities of certain macrobenthic species. Further, it was speculated that ". . . population sizes are largely controlled by predation, and competition for food and space is not important in regulating overall densities under natural circumstances" (Young *et al.*, 1976, p. 588).

In this paper we report on further field experimental manipulations of seagrass-associated macrobenthos in the Indian River estuary, Florida. These experiments were designed to test effects upon densities of macrobenthos by (1) excluding predators by caging, (2) enclosing predators inside cages, (3) adding dense populations of suspension feeders, (4) providing organic enrichment, (5) removing seagrass blades, and (6) erecting cages at different times.

2. Study area

The study area was established at a shallow-water, subtidal location in well-sorted sediment (88.0% sand, 9.6% silt, 2.4% clay) with extensive cover of *Halodule wrightii*—part of a continuous band of seagrasses whose areal extent exceeded 500,000 m^2. This site at Link Port (27°32.1′N; 80°20.9′W) is located between two of the three dredged inlets which bisect the barrier island chain forming the bar-built estuary of the Indian River of east central Florida. Tidal flushing at Link Port is aperiodic; the time required to renew one-half of the water is estimated to be on the order of one week to one month, depending on meteorological conditions. The ranges of temperature (11.5 to 32°C) and salinity (17 to 37‰) recorded at this site since 1972 (Young and Young, 1977) were exceeded during these experiments only in January 1976 when water temperatures dropped briefly to 9°C.

The Link Port site was selected from three sites previously studied (Young *et al.*, 1976; Young and Young, 1977) for this field experimental study because of its intermediate position between extremes of temperature, salinity, and tidal fluctuations, and of predation intensity upon the seagrass-associated macrobenthos.

3. Methods

Four replicate rectangular cores of seagrass and sediment (15 cm × 15 cm × 20 cm deep = 4500 cm^3) were taken from the Link Port site from September 1974 to September 1975 at monthly intervals (except during January and August 1975) and from October 1975 to October 1976 on a bimonthly basis. The latter sampling intervals coincide with periods of sampling the field experiments described below. The top of the core sampler was enclosed with 1.0 mm mesh screen to prevent escape of motile epifauna. Core samples were washed through 1.0 mm mesh Nytex screen; specimens were sorted from retained seagrass and detritus; and all macrobenthos (operationally defined as benthic invertebrates retained by 1.0 mm mesh during sampling, screening, and sorting processes) were identified and enumerated after narcotization, staining, fixation, and preservation (for procedural details see Young and Young, 1977).

Each experimental treatment was administered on a 4 meter square area. Uncaged areas were staked off in a manner similar to the caged areas, but were not surrounded by hardware cloth. Cages were constructed of 12 mm mesh hardware cloth, 2 m on a side and 2 m high. Sides of each cage penetrated the sediment to 5 cm depth and extended above highest tidal stages. The outside of all cages was cleaned of detritus and algae as required. There were no observable changes of sediments inside cages and no apparent disruptive influences of the cage structures on water current flow throughout the experiment (see Young and Young, 1977). Core samples were taken away from the cage sides and away from previously sampled areas to prevent overlap and slumping of sediment. At the completion of each experiment, less than one-fifth of the total area of sediment surface in any cage had been sampled.

The descriptions of the experimental treatments and purpose of each are given in Table 1. Ten of the treatments were initiated at the Link Port site in October 1975 and terminated in June 1976. Two additional treatments testing the effect of time upon caging were initiated, one in December 1975 and terminated in August 1976 (Seasonal I), and one in February 1976 and terminated in October 1976 (Seasonal II). Four replicate box cores were taken from each treatment on four occasions, once every two months starting two months after initiation of each experiment.

In an attempt to reduce effects of small predators that can pass through the mesh of caged treatments (see Young *et al.*, 1976), all cages were "swept" with a 6 mm mesh seine every month to remove fish and decapod crustaceans (except for caged fish and caged crab treatments). Uncaged treatments were seined in a similar manner to equalize effects among all treatments. This procedure was not entirely effective, in that burrowing crabs, for example, were not removed by seining. Care was taken in all cases to minimize disturbance to seagrass and the sediment surface.

Experiments in the field, unlike those in the laboratory, leave environmental factors free to vary to the same extent in experimental and control treatments with the exception of the factor (or factors) being manipulated. Field experiments, by their very nature, are logistically difficult and manpower-intensive efforts. Therefore, we decided at the outset to sacrifice replicate experimental treatments in order to maximize the number of treatments, retain relatively large sample size, and provide replicate samples for each treatment in each sampling period.

Differences among means of macrofaunal densities from all treatments were tested with a one-way analysis of variance (ANOVA). An *a posteriori* Student-Newman-Keuls (SNK) multiple comparison test was made if the ANOVA indicated significant differences among means (Sokal and Rohlf, 1969). All other comparisons of effects between caged and uncaged treatments (i.e., biomass of clipped seagrass blades, shell growth of *Mercenaria mercenaria*, robustness of *Capitella capitata capitata*) were made with a Student's t-test. Significance for the ANOVA, SNK test and Student's t-test was chosen at the 95% level of confidence. The data were not transformed.

4. Results

The seagrass-associated macrobenthos at Link Port is dominated by polychaetes, molluscs, amphipods, sipunculids, isopods and tanaids, in that order of relative abundance (Young *et al.*, 1976). The greatest percentage of the macrobenthos are deposit-feeding species (Young and Young, 1977). Large between- and within-year fluctuations of species richness and densities are characteristic of the macrobenthos

Table 1. Descriptions of experimental treatments and purpose of each.

Treatment	Purpose
1) Caged	To inhibit natural predator (operationally defined here as those predators unable to pass through a 12 mm mesh) effects on the macrobenthos.
2) Seasonal I	To test effects of time on caging. Started December 1975.
3) Seasonal II	To test effects of time on caging. Started February 1976.
4) Caged crabs	To intensify effects of a known decapod crustacean predator on the macrobenthos. Two specimens of *Callinectes sapidus* (blue crab) of 12 and 14 cm carapace width were added to the cage. New specimens of similar sizes were added when necessary.
5) Caged fish	To intensify effects of a known fish predator on the macrobenthos. Five specimens of *Lagodon rhomboides* (pinfish), ranging in length from 10-14.5 cm were added to the cage. New specimens of similar sizes were added when necessary.
6) Caged clams	To intesify cropping effects by a dense population of suspension feeders on settling invertebrate larvae of the macrobenthos and to limit effects of natural predators. Two hundred specimens of the clam, *Mercenaria mercenaria,* ranging in length from 2.5-8.0 cm ($\bar{x} \pm S\bar{x} = 5.56 + 0.11$) were marked for growth measurements and added to the cage.
7) Uncaged clams	To test cropping effects (as in 6), but not those of natural predators. Two hundred specimens of the clam *Mercernaria mercenaria,* ranging in length from 1.75-8.0 cm ($\bar{x} \pm S\bar{x} = 5.32 \pm 0.11$) were marked for growth measurements and added to the uncaged clam area.
8) Caged clipped	To test effects of monthly removal of seagrass blades upon the macrobenthos and to limit the effect of natural predators. Blades were clipped with shears at the sediment-water interface every month, attached epibiota removed and quantified; blades were dried at 80°C and biomass measured.
9) Uncaged clipped	To test effects of monthly seagrass blade removal but not those of natural predators. Blades were clipped with shears at the sediment-water interface every month, attached epibiota removed and quantified; blades were dried at 80°C, and biomass measured.
10) Caged Milorganite	To test the effects of monthly applications of processed sewage sludge (Milorganite)* upon the macrobenthos and to limit effects of natural predators. Milorganite was added every month at the sediment surface at a concentration of 567 g/m^2.
11) Uncaged Milorganite	To test effects of sewage sludge (as in 10) but not those of natural predators. Milorganite was added every month at the sediment surface at a concentration of 567 g/m^2.
12) Uncaged	To test effects of the cage structure itself upon natural predators.

* Milorganite is the trade name of processed sewage sludge in granular form from Milwaukee, Wisconsin. The most common use of this product is as a fertilizer for plants with high organic nitrogen requirements. The minimum guaranteed analysis is as follows: total nitrogen (6.00%), available phosphoric acid (4.00%), Fe_2O_3 (7.50%), ZnO (0.10%), and SO_3 (2.50%).

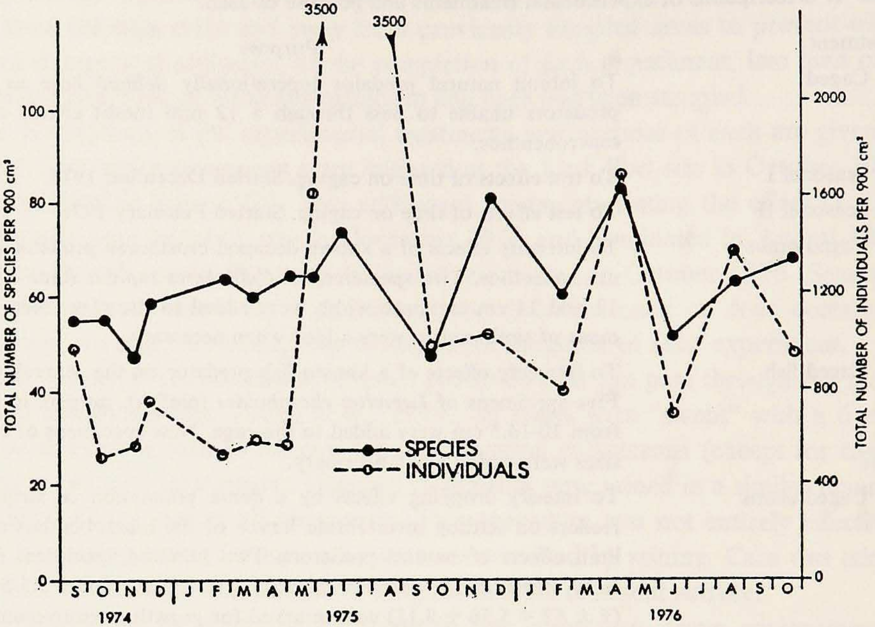

Figure 1. Total number of species (solid line and solid circles) and individuals (dashed line and open circles) per 900 cm² collected from the Link Port site from September (S) 1974 to October (O) 1976.

at this site (Fig. 1). The highly variable nature of estuarine benthic communities is widely recognized (see Boesch *et al.*, 1976).

The standing stock of *Halodule wrightii* in October 1975 was 88.6 g dry/m² from the caged clipped treatment and 86.4 g dry/m² from the uncaged clipped treatment. These values are within the range of standing stock measurements of *H. wrightii* (=*beaudettei*) from Texas at 22-250 ($\bar{x}$=93) g dry/m² (McRoy and McMillan, 1977). There was no significant (Student's t) difference in total biomass of blades from monthly harvesting of the caged and uncaged clipped treatments.

Specimens of *Mercenaria mercenaria* sampled upon termination of the caged and uncaged clam treatments in June 1976 all exhibited shell growth ($\bar{x} \pm S\bar{x} = 6.6 \pm 1.5$ mm). There was no significant (Student's t) difference in shell growth between the two treatments.

When total macrofaunal densities of all species from all experimental treatments were compared with the SNK test, the caged Milorganite treatment had significantly higher densities than all other treatments except for the caged treatment (Fig. 2). Comparisons of densities of total macrofauna from the caged Milorganite treatment with those from the uncaged Milorganite treatment, or both with their respective controls (caged and uncaged treatments), showed no consistent seasonal trends

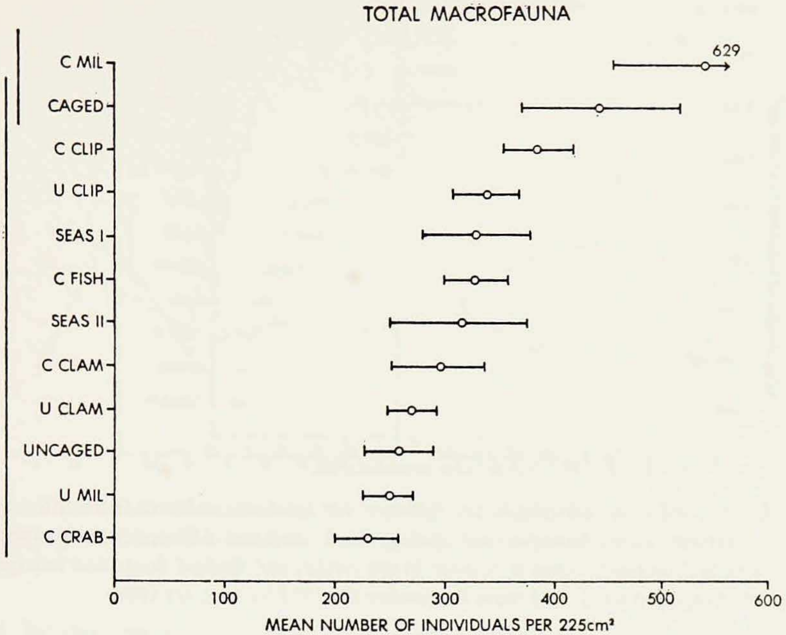

Figure 2. Means (open circles) and standard errors ($\bar{x} \pm S\bar{x}$ = horizontal lines) for number of individuals per 225 cm² for total macrofauna from all treatments. Vertical lines to left of treatment designations encompass groups of means which are not significantly different from one another (at 95% confidence level) by SNK test. The treatment designations are: C MIL = caged Milorganite; CAGED = caged; C CLIP = caged clipped; U CLIP = uncaged clipped; SEAS I = seasonal I; C FISH = caged fish; SEAS II = seasonal II; C CLAM = caged clam; U CLAM = uncaged clam; UNCAGED = uncaged; U MIL = uncaged Milorganite; C CRAB = caged crab.

(Fig. 3). Few or no similarities of trends were seen among the other treatments when compared in a similar manner.

We believe that greater insight into dynamic responses and interactions of the macrobenthos is provided when individual species contributions to overall densities are evaluated. For example, the initial peak of total macrofaunal densities in December 1975 from both the caged Milorganite and caged treatments (Fig. 3) was due largely to the amphipod, *Melita nitida*, which contributed over one-third of the overall species densities in both cases. Likewise, the polychaete, *Capitella capitata capitata*, accounted for 59% of all macrofauna sampled from the caged Milorganite treatment but only 3% from the caged treatment during the April 1976 sampling period (Fig. 3).

Clearly, grouping all species as a "community" masks individual species responses to the experimental treatments. To clarify these different responses, we selected the 11 most abundant species from among 197 species consisting of more than 64,000

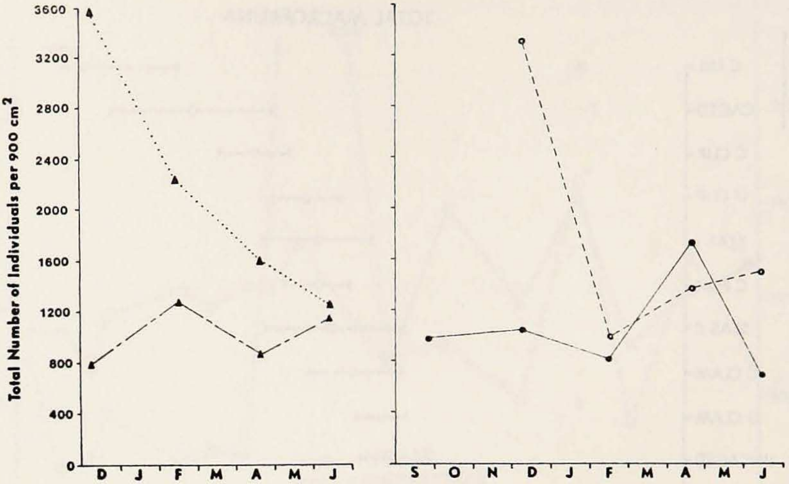

Figure 3. Total number of individuals per 900 cm² for total macrofauna from the caged Milorganite treatment (open triangles and dotted line), uncaged Milorganite treatment (solid triangles and broken line), caged treatment (open circles and dashed line), and uncaged treatment (solid circles and solid line) from September (S) 1975 to June (J) 1976.

individuals (the species list is available from the authors upon request). All 11 species comprised 50% or more of the total densities of macrofauna sampled in every experimental treatment. These 11 species are: the polychaetes 1) *Capitella capitata capitata*, 2) *Streblospio benedicti*, 3) *Laeonereis culveri*, 4) *Polydora ligni*, 5) *Tharyx annulosus*, and 6) *Clymenella mucosa*; 7) the sipunculid *Phascolion cryptus*; the gammaridean amphipods 8) *Melita nitida*, 9) *Grandidierella bonnieroides*, and 10) *Cymadusa compta*; and 11) the gastropod *Diastoma varium*.

The same 11 species given above, with the exception of *Diastoma varium*, were among the top-ten most abundant species from either inside or outside exclosures at Link Port in a 1974-75 caging study (Young and Young, 1977). (For comparison with our previous study, *Cymadusa compta* = *Cymadusa* sp. A, *Grandidierella bonnieroides* = *Grandidierella* sp. A, and *Phascolion cryptus* = *Phascolion* sp.). The most conspicuous omission from these 11 species is the gastropod, *Cerithium muscarum*, which was the second most abundant species at this site from both caged and uncaged samples in the previous study. The density decrease of *C. muscarum* during 1975-76 was not surprising. Year-to-year fluctuations of abundances of this species due, in large part, to intense predation by xanthid and portunid crabs and the carnivorous gastropod, *Melongena corona*, have been documented in the Indian River estuary (Lund, 1976).

Capitella capitata capitata (Fig. 4). This polychaete is a burrowing deposit feeder which maintained relatively constant population levels throughout the year as in-

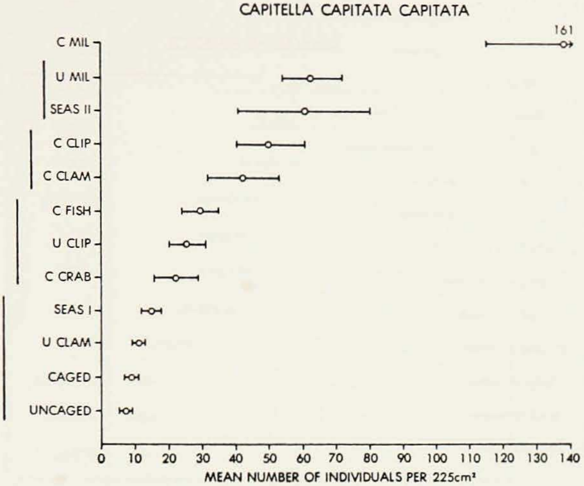

Figure 4. Means and standard errors for number of individuals per 225 cm² for *Capitella capitata capitata* from all treatments. See Fig. 2 for symbols and designations.

dicated by our routine sampling at this site. Densities of this species increased greatly following the addition of Milorganite in the caged area. The caged Milorganite treatment had significantly (SNK) higher densities of *C. capitata capitata* than all other treatments. Both the caged and uncaged Milorganite treatments had significantly (Student's t) more "robust"[3] specimens compared with caged and uncaged treatments. Specimens from the uncaged Milorganite treatment were significantly (Student's t) more "robust" but significantly (SNK) less dense than specimens from the caged Milorganite treatment.

Many studies of the macrobenthos do not distinguish among subspecies of *Capitella capitata*. When we combined densities of *C. capitata capitata, C. capitata ovincola* and *C. capitata tripartita* in order to estimate maximum population sizes of this species from any treatment, densities of *C. capitata* inside the cage with Milorganite (caged Milorganite treatment) reached 10,588 per m² in April 1976, compared with 4,377 per m² from the uncaged Milorganite treatment in February 1976.

Lowest densities of this species occurred in the caged and uncaged treatments as well as two other treatments. Seasonal effects are suggested by significant (SNK) differences of densities of *C. capitata capitata* between both caged and Seasonal I treatments compared with Seasonal II.

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[3] To test the observation that specimens of the polychaete *C. capitata capitata* from caged and uncaged Milorganite treatments were more "robust" as well as more numerous than the same species from caged and uncaged treatments, specimens were pooled, randomly selected and measured for each sampling time and for each of the 4 treatments. Many of the specimens lacked posterior ends, making length measurements of little value. "Robustness" is defined here as the width of the thoracic region at the level of the 5th setiger.

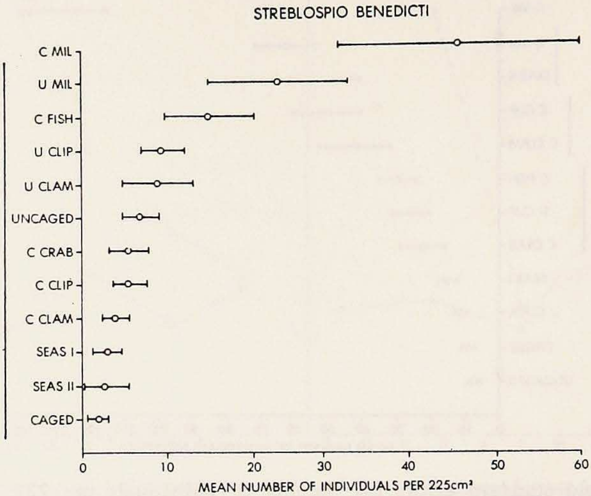

Figure 5. Means and standard errors for number of individuals per 225 cm^2 for *Streblospio benedicti* from all treatments. See Fig. 2 for symbols and designations.

Streblospio benedicti (Fig. 5). *Streblospio benedicti* is a deposit feeder, living in a membranous burrow in the sediment and feeding at the surface by means of long grooved palps. Densities of this spionid polychaete in the caged Milorganite treatment were significantly (SNK) higher than in all other treatments. Described as an opportunistic species (Grassle and Grassle, 1974), *S. benedicti* might be expected to have higher overall densities in caged versus uncaged treatments, as reported in Chesapeake Bay by Virnstein (1977). In the Indian River estuary, the addition of Milorganite to a cage had a greater effect upon this species than Milorganite addition or caging alone.

Laeonereis culveri (Fig. 6). *Laeonereis culveri* is a burrowing deposit feeder. The addition of Milorganite to a cage resulted in significantly (SNK) greater densities of this nereid polychaete than in all other treatments. Densities of *L. culveri* inside the Milorganite treated cage increased from 11% of total macrofauna in April to 22% in June 1976 compared to an increase from 1% to 2% inside the caged treatment (Fig. 3), which suggests a continuing "enhancing" effect of organic enrichment. The significant (SNK) difference in densities of *L. culveri* in caged and uncaged Milorganite treatments suggests greater predation on this species in the uncaged area.

Polydora ligni (Fig. 7). This sedentary spionid polychaete lives in a fragile membranous burrow and feeds at the sediment surface by means of long palps which carry food particles to the mouth. The density of *Polydora ligni* was significantly

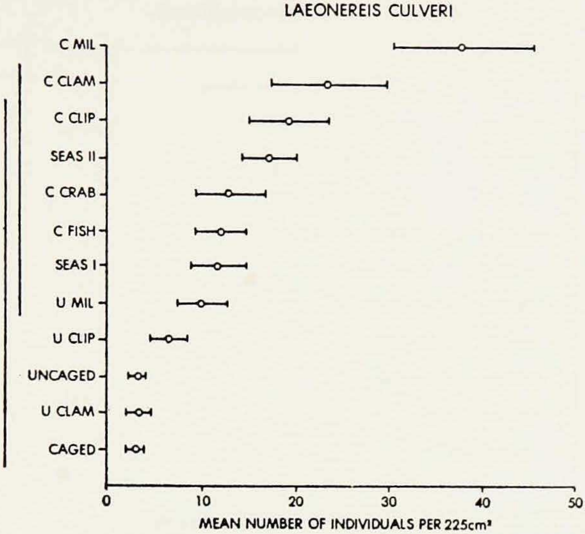

Figure 6. **Means and standard errors for number of individuals per 225 cm² for *Laeonereis culveri* from all treatments. See Fig. 2 for symbols and designations.**

(SNK) higher in the Seasonal I and Seasonal II treatments than in all other treatments. Significant increases in densities of *P. ligni*, particularly during periods of larval settlement, have also been shown inside cages in Chesapeake Bay (Virnstein, 1977; Orth, 1977).

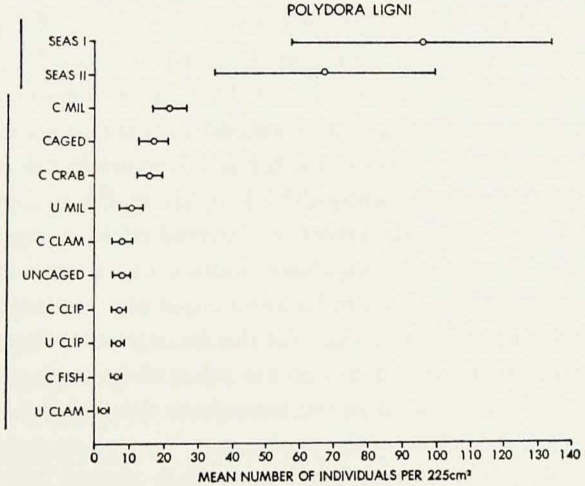

Figure 7. Means and standard errors for number of individuals per 225 cm² for *Polydora ligni* from all treatments. See Fig. 2 for symbols and designations.

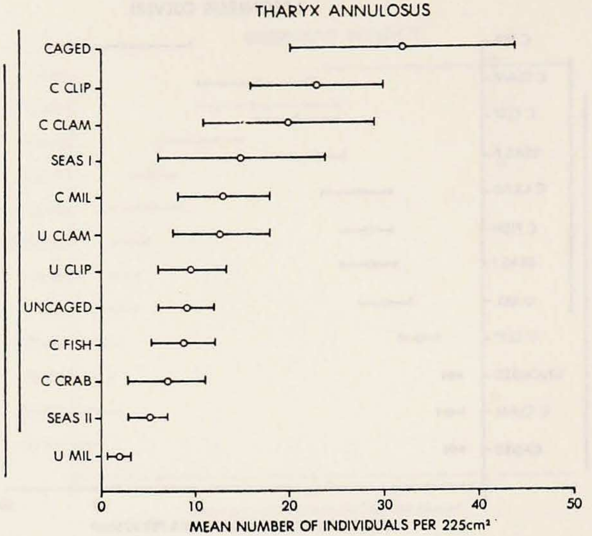

Figure 8. Means and standard errors for number of individuals per 225 cm² for *Tharyx annulosus* from all treatments. See Fig. 2 for symbols and designations.

Tharyx annulosus (Fig. 8). This sedentary deposit-feeding polychaete lies buried in the sediment with its grooved tentacular filaments extended over the sediment surface. The density of *Tharyx annulosus* in the caged treatment was significantly (SNK) higher than in the uncaged Milorganite treatment. All other treatments were not significantly different from one another. High within-sample (between-replicate) variances suggest a patchy distribution of this species.

Clymenella mucosa (Fig. 9). Densities of *Clymenella mucosa* in caged and uncaged Milorganite treatments were not significantly (SNK) different from all other treatments (except the uncaged clipped treatment). This response is in contrast with other deposit-feeding polychaete species (e.g., *Capitella capitata capitata, Laeonereis culveri*, and *Streblospio benedicti*) which had highest densities in the caged Milorganite treatment. Densities were significantly (SNK) higher in the uncaged clipped treatment than in all but four other treatments. The overall effect of caged *versus* uncaged treatments upon densities of this polychaete species was inconsistent, regardless of the time a cage was erected. The reproductive method of *C. mucosa*, i.e., the deposition of eggs in a jelly-mass, may account for this inconsistent effect and high within-sample variance. When the young worms are released from the jelly, they tend to settle and construct tubes of sand in the immediate vicinity of the jelly-mass, thus producing a patchy distribution of this species.

Specimens were abundant in uncaged treatments during June 1975 when *C. mucosa* accounted for 17% of the peak seen in Figure 1, and abundant again in April 1976 when 36% of total macrofauna sampled was this species.

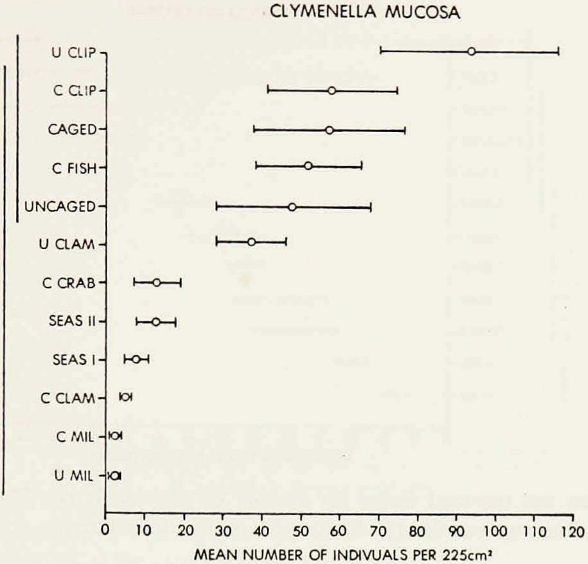

Figure 9. **Means and standard errors for number of individuals per 225 cm² for *Clymenella mucosa* from all treatments. See Fig. 2 for symbols and designations.**

Clymenella mucosa is a "conveyor-belt" deposit feeder (Rhoads, 1974) passing fecal material upwards, with its tube extending as much as 1 cm above the sediment surface. The posterior end of this species is readily cropped by predators without destroying the animal; the animal then regenerates the missing portion to regain its normal complement of exactly 22 segments. During 1974, a study of 829 specimens of *C. mucosa* from the Indian River showed evidence of active regeneration of "tails" in 46% of all specimens examined (Young and Young, unpublished data).

Phascolion cryptus (Fig. 10). The sipunculid, *Phascolion cryptus*, maintained relatively high population densities throughout the year, contributing 8%, 16%, and 22% respectively to the July 1975, April 1976, and August 1976 peaks seen in Figure 1. Significantly (SNK) higher densities occurred in uncaged and caged clipped treatments than all but three other treatments. The effect upon *P. cryptus* of removing the grass blades seems unrelated to what is known about the autecology of this species. *Phascolion cryptus* has direct development with crawl-away juveniles which inhabit empty gastropod shells. Adult specimens are relatively immobile and feed from a buried position in the sediment upon detrital material at the sediment surface with an introvert-type of buccal apparatus. This species may also filter-feed (Hendrix, 1975).

Phascolion cryptus occurred in greatest densities in the same six treatments (although not in the same order) as *Clymenella mucosa.* Neither species responded

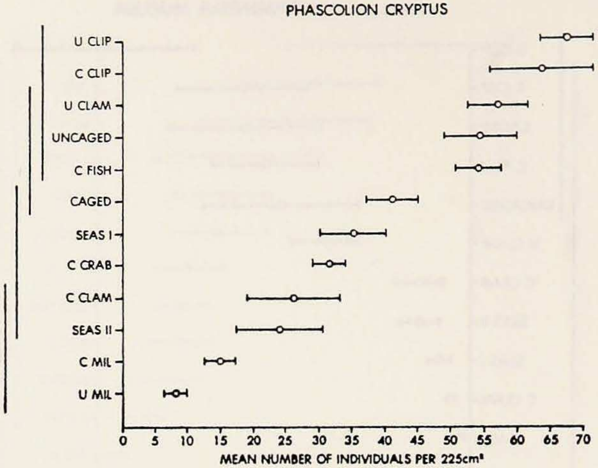

Figure 10. Means and standard errors for number of individuals per 225 cm² for *Phascolion cryptus* from all treatments. See Fig. 2 for symbols and designations.

significantly to the Milorganite treatments. *Phascolion cryptus* showed no clear-cut "caged" effect and responded inconsistently to the other experimental treatments.

Milita nitida (Fig. 11). There were no significant (SNK) differences[4] among means of densities of *Melita nitida* from any of the treatments because of the high variance associated with each treatment. This gammaridean amphipod species had a highly contagious or patchy distribution. Peaks of abundance were observed from caged (exclosure) treatments in February 1975 (Young and Young, 1977) and again in December 1975 (Fig. 3) when this species comprised 24% and 34% of total macrofauna respectively. This periodicity (seasonal reproduction?) was not found in routine sampling and would not have been apparent if natural populations had not been caged.

The highest density of this species in December 1975 resulted from the caged Milorganite treatment (1248 individuals per 900 cm²). Seagrass areas treated with Milorganite experienced high production of epiphytes upon which *M. nitida* would thrive (R. Zimmerman, personal communication), especially when protected from predators. This density of *M. nitida* is higher than from any benthic sample taken from the Indian River estuary over the period, 1973-77 (Indian River Coastal Zone Study, unpublished data).

Grandidierella bonnieroides (Fig. 12). The seven highest densities of this gammaridean amphipod were from caged treatments, the uncaged Milorganite treatment

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[4] Significant differences, however, were found among all treatments with the *a priori* ANOVA test. This result is consistent with the expectation of higher sensitivity of the *a priori* test than the *a posteriori* SNK test for detecting differences among many means (Sokal and Rohlf, 1969).

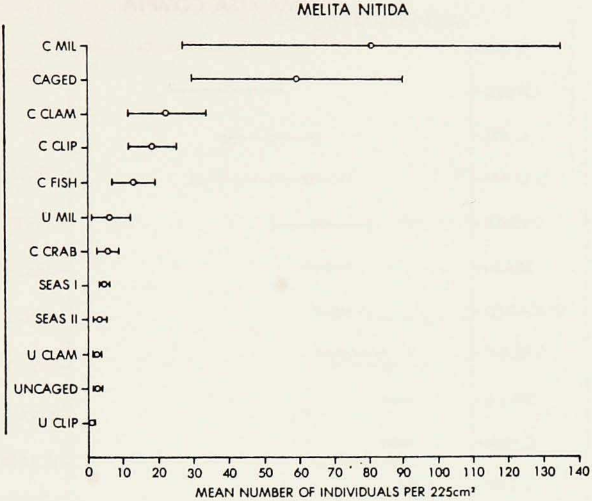

Figure 11. Means and standard errors for number of individuals per 225 cm² for *Melita nitida* from all treatments. See Fig. 2 for symbols and designations.

excepted. Densities of *Grandidierella bonnieroides* were significantly (SNK) higher in the caged treatment than in all uncaged treatments, again except for the uncaged Milorganite treatment. Zimmerman (personal communication) has shown experimentally that *G. bonnieroides* feeds preferentially upon seagrass detritus, eating epiphytic algae only occasionally.

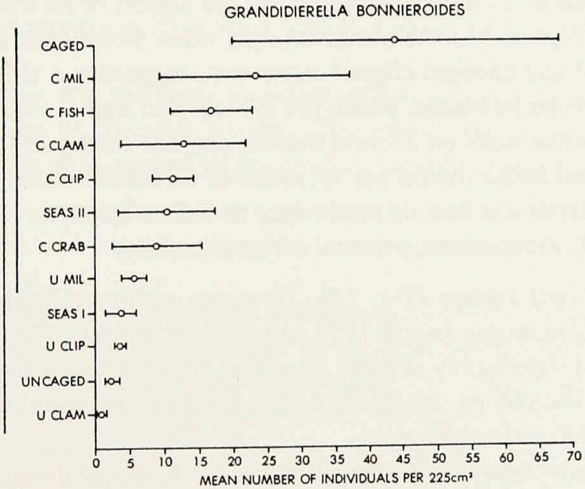

Figure 12. Means and standard errors for number of individuals per 225 cm² for *Grandidierella bonnieroides* from all treatments. See Fig. 2 for symbols and designations.

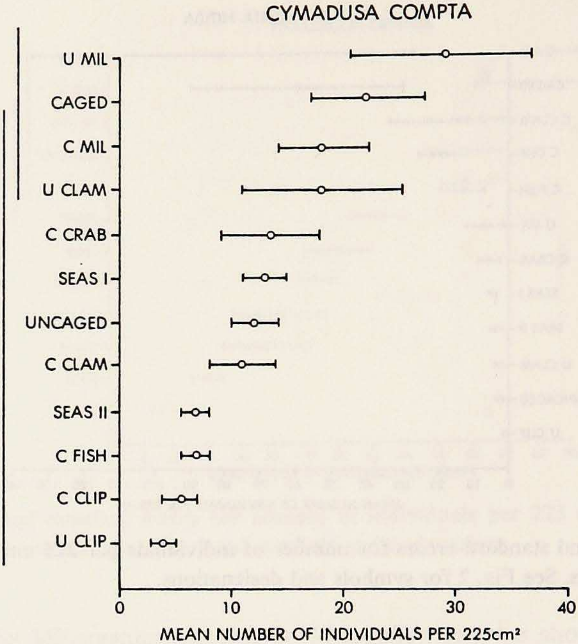

Figure 13. Means and standard errors for number of individuals per 225 cm² for *Cymadusa compta* from all treatments. See Fig. 2 for symbols and designations.

Cymadusa compta (Fig. 13). This gammaridean amphipod species showed no clear-cut differences between caged and uncaged treatments. In the uncaged Milorganite treatment, densities of *Cymadusa compta* were the highest of all treatments and significantly (SNK) higher than the means of eight other treatments. Lowest densities occurred in caged and uncaged clipped treatments, suggesting a close association of this species with seagrass blades. Marsh (1973) reported that *C. compta* is sedentary and inhabits web-like nests on *Zostera marina* seagrass blades in Chesapeake Bay. A more generalized feeder than either *M. nitida* or *G. bonnieroides, C. compta* feeds upon seagrass detritus and floating macroalgae as well as epiphytic algae on *Halodule wrightii* blades (R. Zimmerman, personal communication.)

Diastoma (=Bittium) varium (Fig. 14). *Diastoma varium* comprised 57% of all macrofauna sampled during July of 1976 and 29% in August 1976 (Fig. 1). Overall, densities were not significantly affected by caging *per se*. Using a two-way ANOVA, Buzas (in press) showed no significant caging effects of *D. varium*; however, there were significant differences with time.

The caged clipped treatment had significantly (SNK) lower densities of *D. varium* than three other treatments. As in the case of the amphipod, *Cymadusa compta,* lowest overall densities of *D. varium* occurred in the caged and uncaged clipped

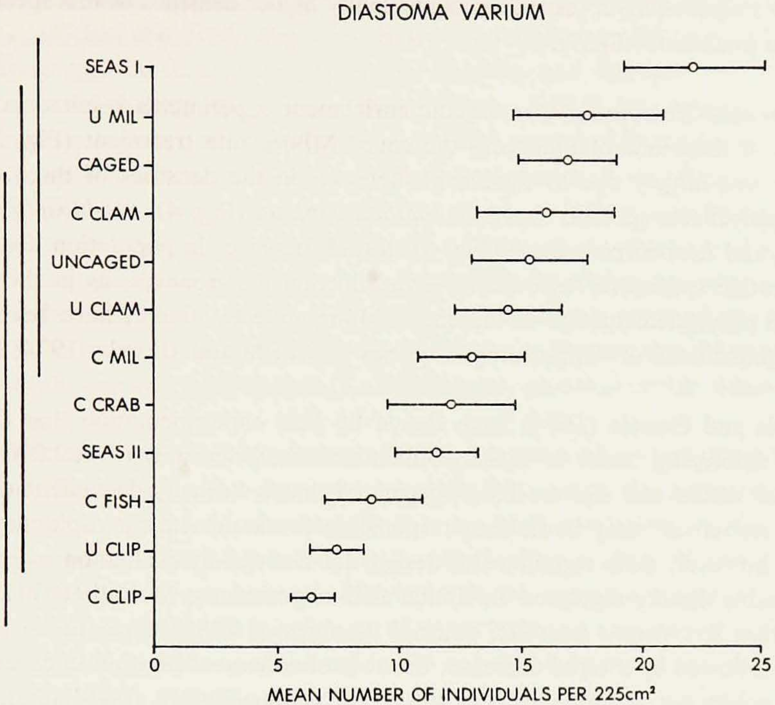

Figure 14. Means and standard errors for number of individuals per 225 cm² for *Diastoma varium* from all treatments. See Fig. 2 for symbols and designations.

treatments. *Diastoma varium* feeds upon epiphytes and seagrass detritus (Adams and Angelovic, 1970).

Diastoma varium was the most abundant macrobenthic species collected from clipped grass blades of *Halodule wrightii*. This observation suggests a "cropping" effect upon densities of *D. varium* by the monthly removal of blades from the clipped treatments.

5. Discussion

a. Seasonal treatments. Large annual fluctuations of overall densities of macrobenthos at the Link Port site are apparent on the basis of the two years of sampling reported here (Fig. 1). Macrobenthic opportunists are largely responsible for this high variability with time (Young, *et al.*, 1976). As expected, our experimental results demonstrate large increases in densities of a macrobenthic species when cages (exclosures) are established at times of peak reproductive activity of that species. For example, cages erected in December (Seasonal I treatment) and in February (Seasonal II treatment), coinciding with the late Winter-early Spring reproductive period of *Polydora ligni*, resulted in significantly higher densities of this species than any other treatment (Fig. 7).

b. Milorganite treatments. Our organic enrichment experiments resulted in highest densities of total macrofauna from the caged Milorganite treatment (Fig. 2). This response was largely due to significant increases in the densities of three deposit-feeding polychaete species, *Capitella capitata capitata* (Fig. 4), *Streblospio bendicti* (Fig. 5), and *Laeonereis culveri* (Fig. 6). Rapid increases in population densities of macrobenthic species in response to environmental disturbances, as in the case of the three polychaete species in the caged Milorganite treatment, have been shown to be characteristic of "opportunistic species" (Grassle and Grassle, 1974; McCall, 1977).

Grassle and Grassle (1974) have shown by field experimentation that *Capitella capitata* colonizing boxes of azoic sediments reached densities of 400,000 per m^2 or greater within one month. They speculated that a "density-dependent depletion of food resources" may have been responsible for a subsequent rapid population decline; however, their experimental design did not permit evaluation of predation as a possible density regulator. In similar field experiments, McCall (1977) demonstrated that *Streblospio benedicti* reached densities of 418,315 per m^2 in less than 10 days followed by a rapid decrease. Because of enhanced siltation in caged boxes, McCall could not separate relative effects of sedimentation, food-limitation, and natural predation upon densities of macrobenthic species.

From our measurements of *Halodule wrightii* biomass taken during the clipped treatment experiments, we estimate a 5-fold annual turnover of photosynthetic standing crop resulting in the production of as much as 435 g dry of seagrass detritus per m^2 each year at the Link Port site. This yield of detritus, although not large in comparison with that produced by seagrasses from some other subtropical areas (McRoy and McMillan, 1977), is dispersed over a long growing season, thus assuring a stable, long-term source of food in the detritus-based food web. Levinton (1972) postulated that such a predictable food supply, "buffered" *via* a microbiologically-mediated food reservoir, would result in food limitation for deposit feeders. Some field studies have provided evidence to support this hypothesis of food limitation of densities (Newell, 1965; Driscoll, 1975; Levinton, 1977) and biomass (Ansell and Trevallion, 1967; Longbottom, 1970) of certain deposit-feeding macrobenthic species. Raymont (1947, 1949, 1950) demonstrated increases in standing crop of macrobenthos resulting from artificial fertilization of sea lochs in Scotland. Further evidence may be derived from "natural experiments" (Connell, 1975) resulting from organic enrichment of inshore marine waters by domestic sewage. Since Blegvad (1932) first reported an abundance of "unusually high-fed" deposit-feeding polychaetes in the vicinities of sewage outfalls from Copenhagen, others (e.g. Anger, 1975; Orlob and O'Leary, 1977) have shown increased densities and biomass of certain macrobenthic species in relation to sewage-enriched areas of the sea floor as long as sufficient dissolved oxygen levels are maintained (see O'Connor, 1972).

That food may be limiting to population densities and biomass of *C. capitata* in a detritus-rich habitat seems a paradox. Tenore (1975) has shown, however, from laboratory cultures of *C. capitata* that detritus produced from *Zostera marina* seagrass is a poor food, in comparison with others, because of its refractory nature. Tenore (1977) has recently demonstrated that seagrass detritus is nutritionally deficient in nitrogen content. We suggest that the addition of nitrogen-rich Milorganite to detrital food resources at Link Port was responsible for higher densities and more "robust" individuals of *C. capitata capitata.* Specimens of this species from the Link Port site have been raised successfully in laboratory cultures using Milorganite as the substratum and sole food source (K. Eckelbarger, personal communication).

c. Enclosure and exclosure experiments. Adding known predators to cages had less effect upon the macrobenthos than we expected. As is often the case when active predators are confined to enclosures, there were high mortalities of the pinfish, *Lagodon rhomboides* (caged fish treatment) and the blue crab, *Callinectes sapidus* (caged crab treatment); specimens had to be replaced on a routine basis. There is also the possibility that feeding behavior of caged animals was modified. Densities of *L. rhomboides* that were maintained in the caged fish treatment ($\leqslant$ 1.2 fish per m^2) were lower than naturally occurring densities of this species at Link Port (G. Gilmore, personal communication). Furthermore, the densities of *C. sapidus* that were experimentally maintained in the caged crab treatment ($\leqslant$ 0.5 crabs per m^2) were low in relation to populations of other decapod crustaceans inside all cages. Virnstein (in press) has experimentally and independently substantiated the hypothesis of Young *et al.*, (1976) that the densities of decapod predators increase significantly inside cages in the Indian River estuary and that a cage serves as a refuge for decapods from their own predators. We conclude, therefore, that neither predator enclosure experiment was sufficiently effective for the purposes intended.

Space may become a limiting resource for certain infaunal macrobenthic species inside cages. For example, Virnstein (1977) suggested that space was limiting when extrapolated densities of *Streblospio benedicti* reached 140,000/m^2 inside cages in a subtidal sandy habitat in Chesapeake Bay. Extrapolated maximal densities of total macrobenthos in this study, i.e. December 1975 densities of 40,000 individuals per m^2 from the caged Milorganite treatment, indicate to us that space *per se* was not limiting in any of the experimental treatments. This is not to say, however, that competitive interactions between species (see Woodin, 1974, 1975) did not occur. Considering the paucity of information on life histories of macrobenthic species discussed here, we have chosen not to "make the right prediction for the wrong reason" (Dayton, 1973) by postulating competitive interactions between species on the basis of these experimental results.

d. Clam treatments. Instances of destruction of macrobenthic larvae by suspension-feeding bivalves have been cited by Kristensen (1957), Thorson (1966), Ziegelmeier (1970) and Mileikovsky (1974). These and other observations support Woodin's (1976) prediction that "No infaunal forms should consistently attain their highest densities among densely packed suspension-feeding bivalves." Results from our caged and uncaged clam treatments provide no experimental substantiation of this prediction. High densities of large specimens of the bilvalve, *Mercenaria mercenaria,* used in these experimental treatments (50 clams per m^2) had no measurable effect upon macrofaunal densities. In the uncaged clam treatment low densities of *Polydora ligni* (a polychaete with pelagic larvae) are accompanied by similar low densities of *Grandidierella bonnieroides* (an amphipod with direct development). In either case these low densities are significantly different from those in many other treatments (Figs. 7, 12) and provide no conclusive information about "larval cropping" by the suspension feeders.

e. Clipped treatments. The gastropod *Diastoma varium* and the amphipod *Cymadusa compta* are closely associated with and occur in high densities upon seagrass blades, although both species are also collected in lower numbers from sediment among seagrasses (Marsh, 1973; Orth, 1973). In our clipped treatments both species showed greatly decreased densities (Figs. 13, 14). The fact that both species were found in abundance in clipped grass samples supports the supposition that the clipping treatment itself "cropped" population densities (see Results).

The high densities of the sipunculid *Phascolion cryptus* (Fig. 10) and of the polychaete *Clymenella mucosa* (Fig. 9) from both clipped treatments are less readily explained. This result is curious in terms of their dissimilar feeding strategies: One, *P. cryptus,* is a versatile surface deposit and filter feeder; the other, *C. mucosa,* feeds selectively on buried deposits (see Results). *Clymenella mucosa* shows highest densities in association with *Halodule* (=*Diplanthera*) *wrightii* from Tampa Bay (Santos and Simon, 1974) and from Biscayne Bay (O'Gower and Wacasey, 1967) in Florida. Furthermore, highest densities of *Phascolion cryptus* (=*Phascolion* sp, "a", O'Gower and Wacasey, 1967, in Hendrix, 1975) from Biscayne Bay are associated with *Halodule wrightii.* The manner in which increased densities of these 2 species are related to the removal of grass blades by clipping is not clear. Perhaps a relationship with the sediment stabilizing effect by grass rhizomes, unaffected by the clipping treatment, rather than the blades is the critical factor (see Orth, 1977). Predation appears to be relatively unimportant in the regulation of densities of both species, as shown by our caging results. As suggested by results of the uncaged clipped treatment for both species, greater "vulnerability" of these potential prey in the absence of a refuge that seagrass blades may provide is not an issue. We conclude that some requisite for these species is enhanced by clipping in a manner not currently explainable by what is known of their life histories.

6. Conclusion

It is apparent from these field experiments that individual macrobenthic species respond in a variety of ways to the various treatments. Densities of some species increase markedly with organic enrichment (*Capitella capitata capitata, Streblospio benedicti, Laeonereis culveri*), one in terms of the time when a cage is erected (*Polydora ligni*), and some with the clipping of grass (*Phascolion cryptus, Clymenella mucosa*). Other species, (*Diastoma varium* and *Cymadusa compta*), closely associated with seagrass exhibit decreased densities when seagrass blades are removed. The relative importance of predation upon densities of seagrass-associated macrobenthos is clearly different for each species.

"Important," i.e. numerically dominant, macrobenthic species from routine benthic surveys are often singled out for analysis on the basis of their greater abundance compared with other less numerous species. It appears from our caging experiments however, that certain macrobenthic species (e.g. *Melita nitida, Tharyx annulosus, Grandidierella bonnieroides*), occur in highest densities inside cages. These species may be overlooked entirely in sampling designs which do not take their high vulnerability to predation into account (i.e. the predation rate is so high that such species are cropped too fast to be sampled). It is these macrobenthic species, by definition, which may be most "important" in the trophic dynamics of seagrass ecosystems.

These experimental results may encourage caution on the part of marine ecologists wishing to generalize from one species or group of species to the "community" level of organization. The factors which effectively regulate the density of one species may not affect another. Responses to environmental disturbances by taxonomically distant and trophically dissimilar species may be more alike than by species of the same taxonomic group and feeding type. We suggest that new and innovative experimental approaches both in the field and laboratory, coupled with in-depth studies of the "natural history" of individual species, provide the greatest promise for understanding the dynamics of macrobenthic communities.

7. Summary

(1) Eleven numerically dominant species of macrofauna were selected for statistical comparison of densities in 12 different experimental treatments at the Link Port site.

(2) Densities of the polychaetes *Capitella capitata capitata, Streblospio benedicti* and *Laeonereis culveri* increased markedly with the addition of nitrogen-rich processed sewage sludge (Milorganite).

(3) The polychaete *Polydora ligni* increased densities when the erection of cages coincided with its period of reproductive activity.

(4) When seagrass blades were clipped, the sipunculid *Phascolion cryptus* and the

polychaete *Clymenella mucosa* increased densities, while the gastropod *Diastoma varium* and the amphipod *Cymadusa compta* showed density decreases.

(5) Certain macrobenthic species (e.g. the amphipod *Melita nitida*, the polychaete *Tharyx annulosus*, and the amphipod *Grandidierella bonnieroides*) occurred in highest densities inside predator exclusion cages, suggesting high predation pressure upon these species.

(6) Enclosing predators or dense concentrations of suspension feeders inside cages had no measurable effect upon macrobenthic densities.

(7) The relative importance of predation was clearly different for each of the 11 species selected, varying in terms of the "disturbance" being tested in each experimental treatment.

(8) Caution is urged when extrapolations are made from the species or species group to the community level of organization.

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