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THE EFFECTS OF PREDATION BY EPIBENTHIC CRABS AND FISHES ON
BENTHIC INFAUNA IN CHESAPEAKE BAY

A Dissertation

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment

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Doctor of Philosophy

by

Robert W. Virnstein

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APPROVAL SHEET

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the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

The significance of large mobile predators in controlling the distribution and abundance of infauna in a shallow subtidal sand community was tested using manipulative field experiments. Blue crabs (Callinectes sapidus) and two species of bottom-feeding fishes, spot (Leiostomus xanthurus) and hogchoker (Trinectes maculatus), were either excluded from or confined to small areas using wire mesh cages.

The infauna responded to decreased predation with a large increase in density and diversity within 2 months. The largest population increases were exhibited by opportunistic species, which are considered to be most subject to predation. Species whose populations were least affected by predation were those species which either live deep in or quickly retract into the sediment. These species thus avoid predation and were generally the dominant species in the natural community. For most species, recruitment was by planktonic larvae and growth was very rapid, individuals growing to maturity in only a few months.

All species increased in exclosures, suggesting that their population densities are not controlled by competitive interactions. In this community, infaunal population sizes are limited by predation and not by food or space. Severe predation pressure and physical disturbances, particularly sediment instability, keep population levels far below the carrying capacity of the environment. The severe predation, and the rapid growth, short generation times, and rapid turnover rates of constituent populations, suggests that such infaunal communities, despite a low standing crop, are an important food source for predator species important to man.

EFFECTS OF PREDATION ON AN INFAUNAL COMMUNITY

INTRODUCTION

Soft-bottom communities are extremely important in terms of ecosystem structure and function, nutrient recycling (Davies 1975, Rowe et al. 1975) sediment dynamics (Rhoads and Young 1970, Rhoads 1974), energy flow (Pamatmat 1968, Marshall 1970, Smith 1973, Davies 1975), and are a major food source for epibenthic and demersal predators (Medcof and MacPhail 1952, Smith 1970, Stickney et al. 1975, Arntz and Brunswig 1975), many of which are directly valuable to man.

Many theories of soft-bottom community organization have grown from studies heavily dependent on sampling approaches which stress the descriptive aspects of the community (e.g. Thorson 1957, Sanders 1960, Boesch 1971, 1973, Lie 1974). While this descriptive work is a necessary first step, few experiments have been conducted to identify the functional roles of the major community components of any soft-bottom community. The concept of community structure and organization suggests more than a mere description of the assemblage of populations (Dayton 1971). A better method of determining structure is to experimentally change variables or populations (Connell 1972). To do so requires manipulation such that there are comparable altered (experimental) and unaltered (control) areas. The information gained by such manipulations should indicate the important parameters controlling the community structure and ideally should explain and predict the observed distributional patterns and abundances of the species in the community (Dayton 1971, Connell 1972). In a series of field experiments,

Connell (1961a, b, 1970, 1972), Dayton (1971), Paine (1974), and Menge (1970) have demonstrated clearly that both physical and biological factors are important in determining vertical distribution and abundance of organisms on marine rocky intertidal surfaces.

These experimental studies on rocky intertidal surfaces have several advantages over similar experiments on subtidal soft-bottoms: the rocky areas are accessible; their species are well known; species abundances and distributions can be seen and thus measured or estimated directly without removing the animals; and populations are amenable to experimental manipulation in the field (Connell 1972). In contrast, subtidal soft-bottom areas are less accessible; species cannot be removed easily or selectively; and, most importantly, the infauna of soft bottoms cannot be enumerated without permanently removing some of the animals and substrate, thus disturbing and partly destroying that which was to be measured. Due to these inherent difficulties, ecologists working on soft-bottom infauna are only recently progressing past the stage of community descriptions to assess the role of physical and biotic interactions in community structure. Predation by epibenthic crabs and fish is one such potentially important biotic interaction.

Many studies have shown that demersal fish (Darnell 1958, Bakus 1964, Medcof and MacPhail 1952, Smith 1970, Peer 1970, Arntz and Brunswig 1975, Stickney et al. 1975, McEachran et al., in press) and crabs (Darnell 1958, Landers 1954, Menzel and Hopkins 1955, Dunnington 1956) feed on soft-bottom benthos, including infauna. Although the assumption is often made that a large proportion of infaunal mortality is due to predation, few studies have examined the effect of predation on infaunal communities, particularly subtidally. Woodin

(1974) inadvertently found that crabs could reduce greatly the abundance of tube-building polychaetes in a North Pacific intertidal soft-sediment environment. Naqvi (1968) used 6 mm mesh cages to provide protection from predation to the intertidal infauna at Alligator Harbor, Florida. He found four times as many animals inside the cages as outside the cages. No predators, however, were noted or identified, and it was not demonstrated that results were due to lack of predation.

Many bottom-feeding fishes migrate into Chesapeake Bay and its tributaries in the spring, feed throughout the spring and summer, and then leave the Bay in the fall (McHugh 1967, McErlean et al. 1973). Some of these more abundant species are spot (Leiostomus xanthurus), Atlantic croaker (Micropogon undulatus) and summer flounder (Paralichthys dentatus). The hogchoker (Trinectes maculatus) is a year-round, but migratory, resident. The blue crab (Callinectes sapidus), an especially voracious feeder on the infauna, is very abundant throughout the Bay during summer but is inactive during winter, when it hibernates in the sediment of the deeper waters of the lower Bay.

Shallow-water subtidal communities in Chesapeake Bay have low infaunal densities compared to similar but vegetated sediments (Orth, 1973), where crabs have difficulty digging through the rhizome mat of submerged grasses. Also, these densities are lowest in summer and fall (when crabs and fish have been feeding on the infauna) and highest in winter and spring (when these predators are absent), suggesting an inverse functional relationship between intensity or duration of predation and infaunal abundance.

This thesis reports the results of manipulative field experiments to test the significance of large mobile predators in controlling

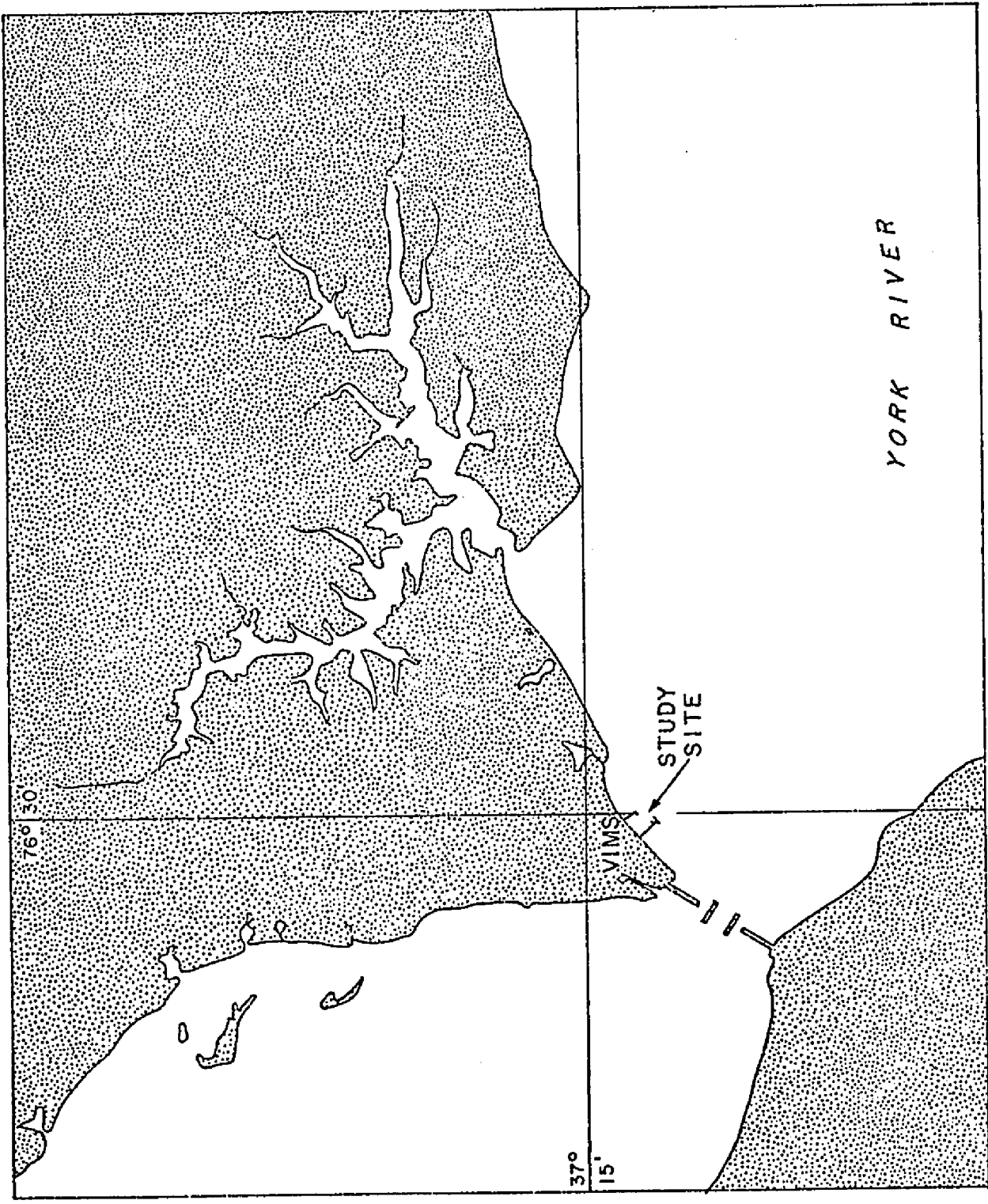
the distribution and abundance of infauna in shallow subtidal communities.

METHODS AND MATERIALS

The area investigated was a shallow (1.4 m at MLW) sandy bottom 70 m from the mean low water line in the lower York River at the Virginia Institute of Marine Science (Fig. 1). Wire mesh cages were used either to exclude predators from, or to confine certain predators to, a small area. Cages measuring 50 cm square by 15 cm high were constructed of 12 mm (half-inch) mesh wire hardware cloth over a frame of 9 mm-diameter steel rods (Fig. 2). A trap door was cut in the top of each cage to provide access inside the cages. The 30 cm legs and 5 cm of the bottom edge of the sides were pushed into the sediment to keep the cage in place and to prevent predators from digging under the cage. Fouling organisms were removed by scrubbing the cages frequently with a wire brush (weekly scrubbing after the first 3 weeks).

Cages and other treatments were placed 3 m apart at randomly assigned positions of a 4 x 6 grid measuring 12 x 20 m (long axis parallel to shore). In each experiment, all cages and treatments were started on the same date, left for a predetermined period of time, and then sampled on the same date. Preliminary experiments in 1973 showed that significant changes took place within 2 months. Therefore, the experiments in 1974 were run for 2 months. There were two replicates of each treatment. The various treatments were: control (uncaged); empty cage; cage containing a crab; 1 m² cage containing a crab;

Figure 1. Map showing location of study area in the lower York River, Virginia.



YORK RIVER

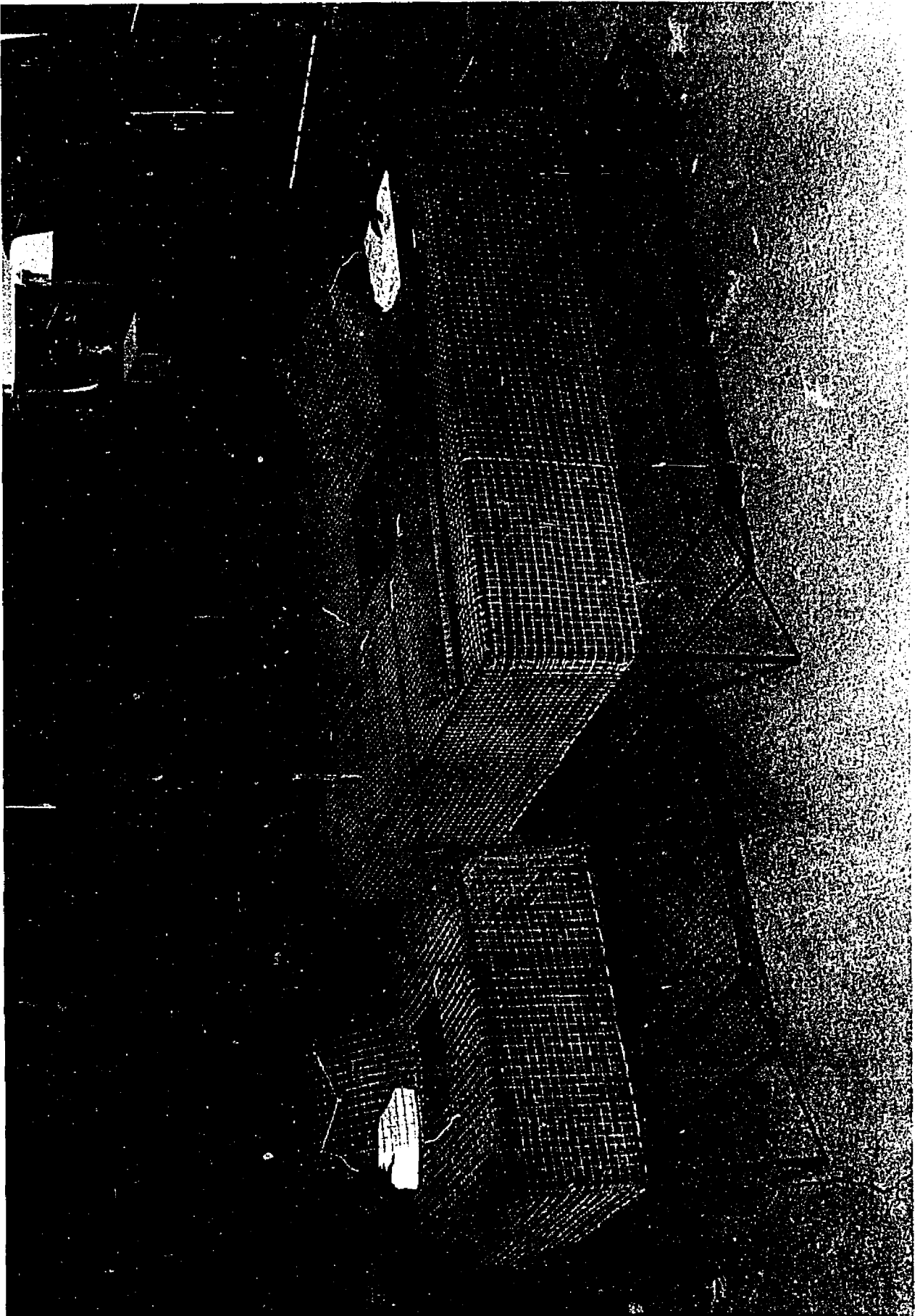
STUDY SITE

VIMS

76° 30'

37° 15'

Figure 2. Photograph of cages. The standard cage used is on the left, the 1 m² cage on the right. When set out, the lower horizontal bar was pushed below the sediment-water interface.



cage divided by mesh into quadrants each containing a crab; cage containing a fish (1973: hogchoker, 1974: spot); cage with the inside sediment manually disturbed; two-sided cage (with top); and a crab tethered to a stake. The crabs used were 9-11 cm carapace width; the spot and hogchokers were 12-13 cm total length. The fish were measured before being put in the cages and then again at the end of the experiment (if they could be recaptured). All fish survived, but no crab survived the full two months of an experiment, having an average life expectancy of one month in the cages. When a crab died, it was replaced by another. Major experiments were run July to September in 1973 and May to July in 1974. Additional empty cages were put in and sampled after 2, 4, 6, 9, and 12 months in 1974. A complete table of treatments and replicates is given before the results of each experiment.

To sample the infauna in a cage, the cage was carefully pulled out of the sediment and set aside. Five cores were taken at randomly assigned positions from within the area where the cage had been. Samples were taken with an 8.1 cm inside diameter (0.005 m^2) hand-held PVC pipe corer to a depth of 10 cm. In 1973, samples were sieved through a 0.5 mm screen and then fixed in formalin with the vital stain phloxine B added. In 1974, samples were fixed in formalin first and then sieved. This latter procedure increased the number of animals retained, since many thread-like worms (especially oligochaetes) would crawl through the screen if sieved alive. The retained animals were sorted from the sediment under a dissecting microscope, identified, counted, many measured, and all retained in ethanol. Samples were taken in the same manner from randomly assigned uncaged plots whenever a cage

was put in or sampled, as well as during most other months. All servicing of cages, sampling, and observations were carried out using SCUBA gear.

Samples for analysis of sediments were taken with a 5 cm corer 5 cm deep, and analyzed for particle size according to methods given by Folk (1968). The sand fraction was separated from the silts and clays by wet sieving through a 62 μ mesh sieve and analyzed by dry sieving through a Wentworth sieve series. The silt-clay fraction was measured by pipette analysis. Orange-painted sand was placed on the sediment both inside and outside the cages so that any differences in sediment stability and transport by currents and waves could be observed.

Quantitative analyses of faunal samples were done using the pooled data from both replicates. In the few cases where replicates were quite different, each replicate was treated separately.

Comparisons of total density, number of species, and number of individuals of abundant species were made between the treatments using a one-way analysis of variance (Sokal and Rohlf 1969). Homogeneity of variance was tested using the F_{\max} -test. If a significant departure from homogeneity was found, a $\log(x + 1)$ transformation was applied, and the transformed data then retested with the F_{\max} -test. If the analysis of variance indicated significant differences between means, all means were compared using the a posteriori Student-Newman-Keuls multiple comparison test. A t-test was used to test whether a sample mean was significantly greater than zero. Significance was chosen to be the $\alpha = 0.05$ level. Any departures from this standard procedure are noted.

Basic assumptions of the experimental design

In addition to the standard assumptions of random sampling, adequate sample size, etc., there are two other basic assumptions underlying the scheme of the experimental design. One assumption is that the infauna throughout the area where the cages were placed was homogeneous, i.e. that significant differences did not exist from one small plot to another a few meters away, and when cages were placed over different plots on the same date, that they all originally enclosed the same infaunal community. This assumption was tested by comparing replicates from randomly selected uncaged areas for all months when replicates were taken. Uncaged replicates were taken, in the sense that two uncaged plots the size of a cage were randomly selected and five randomly placed cores were taken from each of the two replicate plots. Total density and number of species per core of replicates were compared using a one-way analysis of variance, and there were no significant differences ($\alpha > 0.05$) between replicates from any one month. Therefore the position of a cage did not have any effect on the infauna within that cage.

The second assumption is that if two cages were put in at the same date, and one cage sampled at time t_1 and another at time t_2 , then both cages had the same infauna at time t_1 . Unfortunately, this assumption was untestable due to the destructive nature of the sampling. Repeated observations of cages, however, partially confirmed this assumption for those species visible at the sediment surface.

RESULTS AND INTERPRETATION

The Natural Community

The area investigated, a shallow, (1.4 m) sandy, unvegetated bottom in the lower York River (salinity 16-23 o/oo) is probably representative of many of the extensive shoal areas of the Chesapeake Bay and its subestuaries. Sediments and communities were similar at 1.5 and 3.0 m-deep sites studied earlier by Haven et al. (1967). Sediments were poorly sorted ($\sigma_I = 1.10 \phi$) fine sands ($Md_\phi = 2.52 \phi = 0.178 \text{ mm}$) (Folk 1968) with a 15% silt-clay content. The sediment surface had a slight topographic relief of 1-2 cm, covered with a layer of fecal pellets, particularly concentrated in the slight depressions (Fig. 3).

Rank analysis (Fager, 1957) was used to determine dominant species based on the ten months of 1974 samples from uncaged areas (Table 1). For each month's sample, the top-ranked species was given 10 points, second-ranked 9 points, etc., for the top 10 species. Maximum possible score (for a species top-ranked in every sample) is 100. Of the top 12 species, 11 are annelids (one oligochaete and 10 polychaetes). The top five species build vertical tubes or burrows in the sediment but exhibit diverse feeding types: two feed on the sediment surface (Spiochaetopterus oculatus and Streblospio benedicti), two feed anterior end down at the bottom of their tubes or burrows (Pelosclex gabriellae and Heteromastus filiformis), and one species is a tentaculate suspension feeder (Phoronis psammophila). Indeed, Phoronis is the only

Figure 3. Profile (top) and vertical (bottom) photographs of natural sediments taken in the field using methods similar to that of Rhoads and Cande (1971), using a hand-held Nikonos camera. Actual field of view is approximately 10 x 12 cm. The predominant feature in the lower photograph is the paired siphons of the angel-wing clam, Cyrtopleura costata (L.).

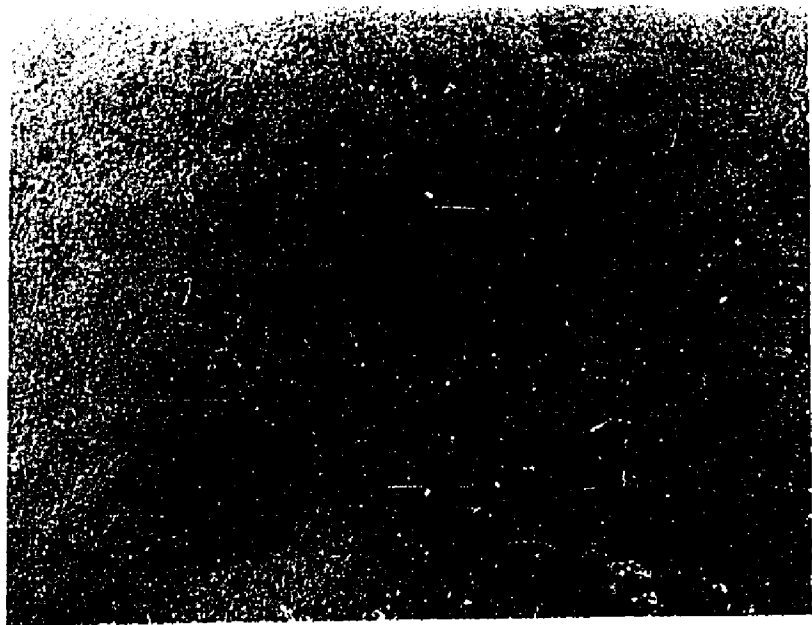
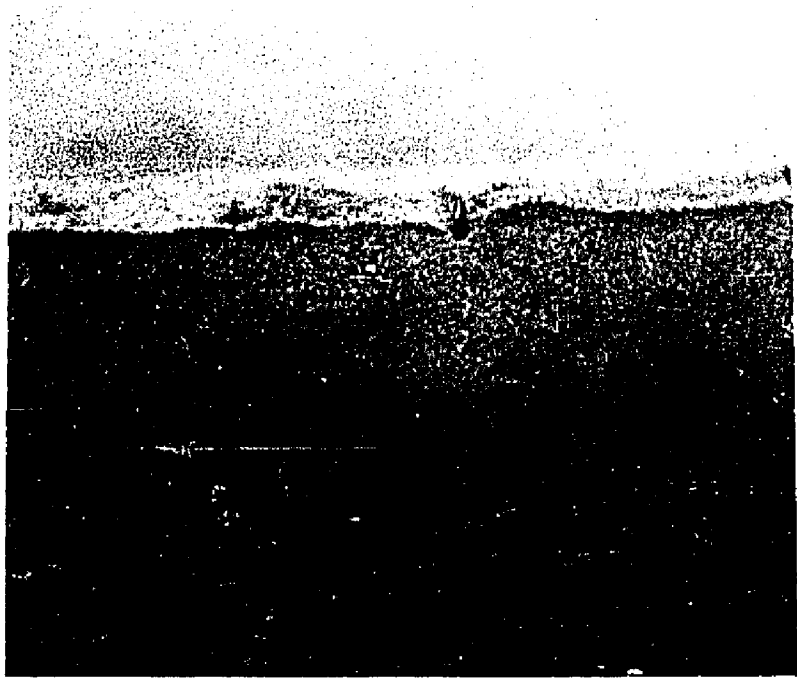


TABLE 1

Rank analysis of dominant species in the natural community based on samples from ten months in 1974.

Species	Rank	Score	Average density (No./m ²)	Variability of density (variance of monthly means about the yearly mean)
<u>Pelosclex gabriellae</u> (O)	1	96	3971	7.03
<u>Spiochaetopterus oculatus</u> (P)	2	80.5	890	0.36
<u>Heteromastus filiformis</u> (P)	3	79	1424	1.00
<u>Streblospio benedicti</u> (P)	4	63	1162	10.06
<u>Phoronis psammophila</u> (Ph)	5	50.8	436	0.68
<u>Glycinde solitaria</u> (P)	6	45.3	349	0.89
<u>Polydora ligni</u> (P)	7	27	450	11.90
<u>Paraprionospio pinnata</u> (P)	8	22.3	167	0.46
<u>Scolelepis squamata</u> (P)	9	15.5	153	0.51
<u>Scoloplos robustus</u> (P)	10	15.3	107	0.54
<u>Eteone heteropoda</u> (P)	11	13	105	1.34
<u>Nereis succinea</u> (P)	12	9.5	110	0.37
<u>Acteon punctostriatus</u> (G)	13	9	89	0.64

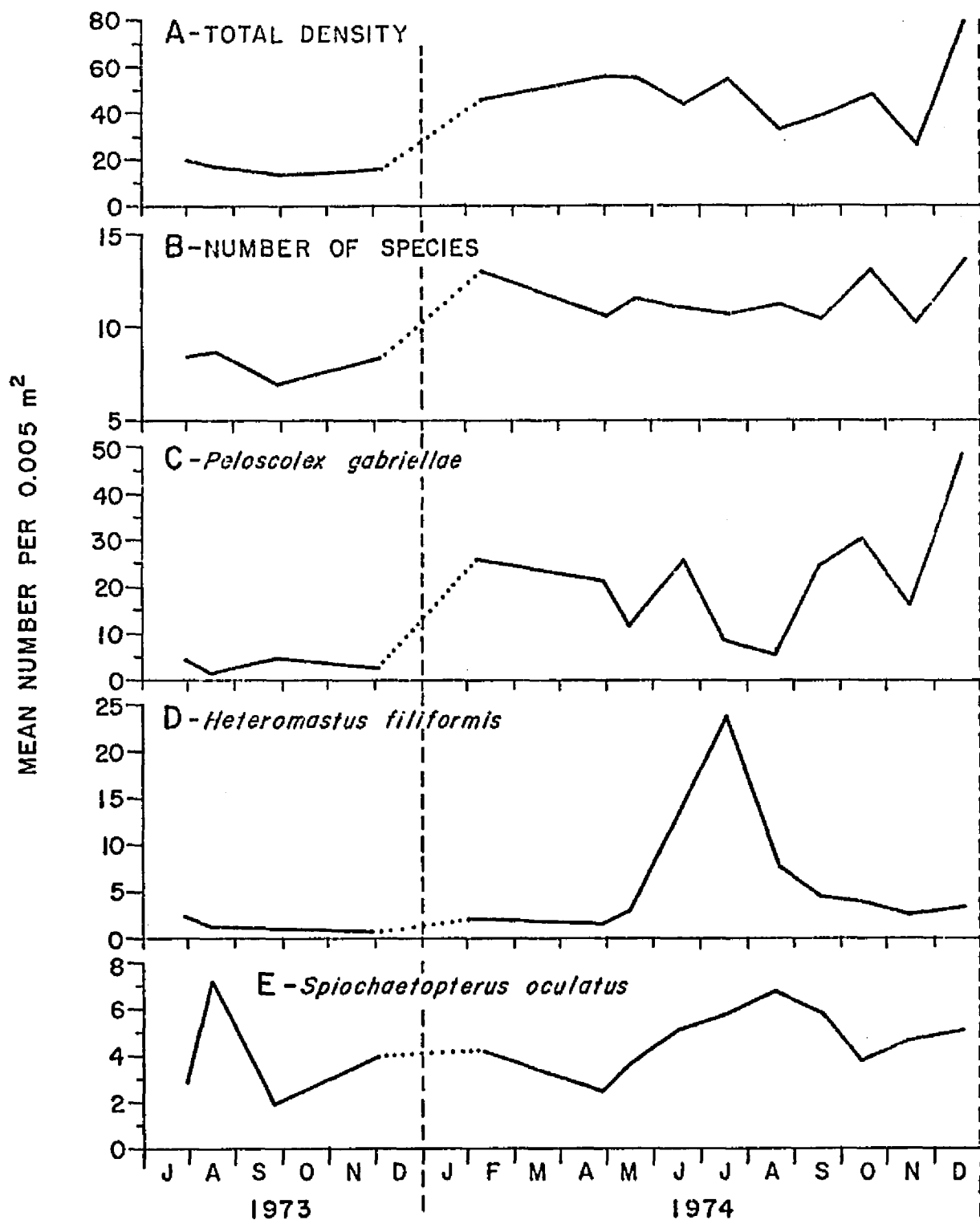
O = oligochaete, P = polychaete, Ph = phoronid, G = gastropod

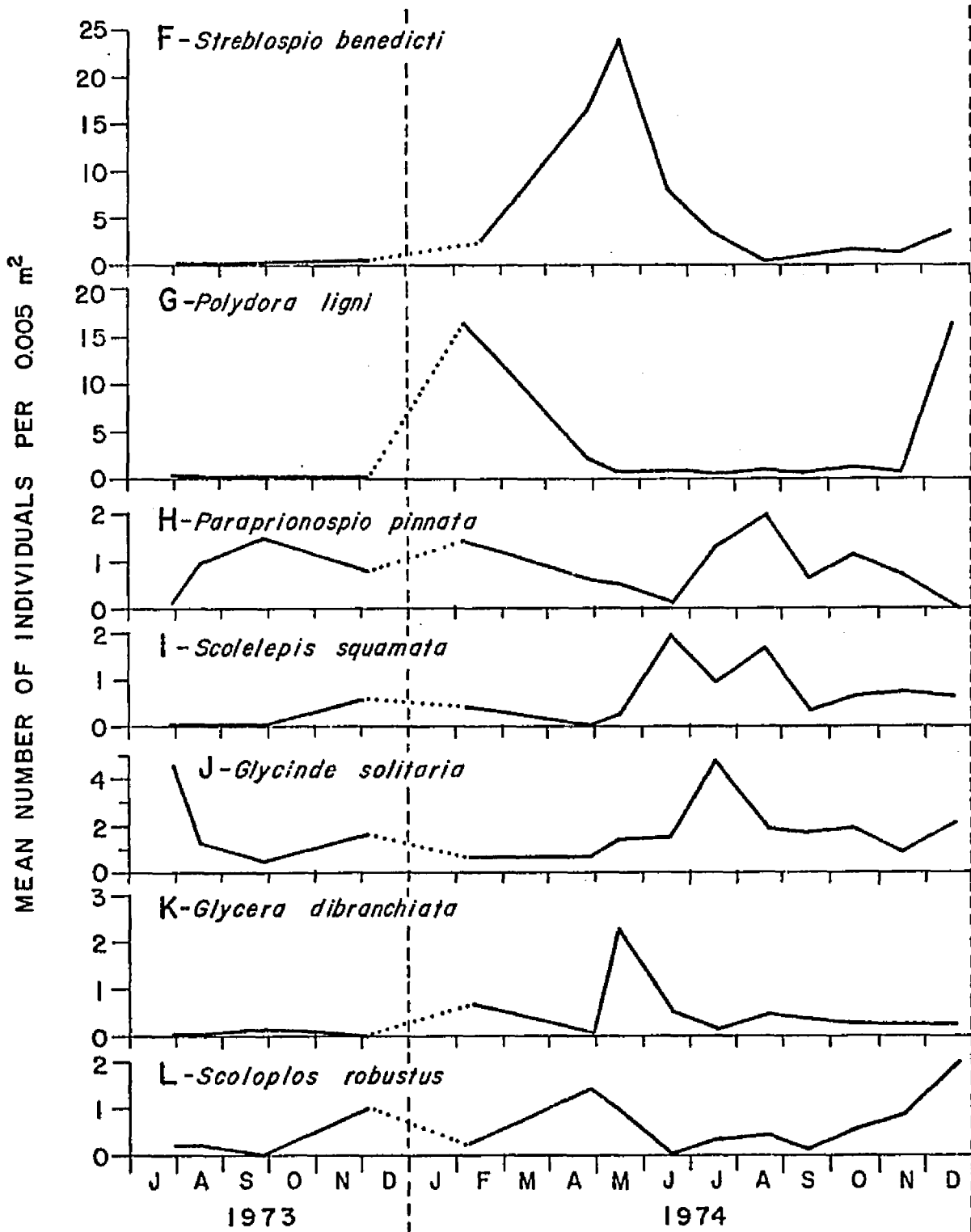
suspension-feeding species of the top 13 species; the other 12 species ingest sediments or surface deposits. Of significant note is the complete absence of bivalves and crustaceans from this list of dominant species.

The ranking of the dominant species was rather constant throughout the year. For example, in the ten samples Peloscolex ranged in rank only from 1-3, Spiochaetopterus ranked 2-5, Heteromastus 1-5, and Glycinde solitaria 4-9. A relative index of persistence, calculated as the ratio of the variance of the monthly means to the yearly mean (Table 1), indicates that Spiochaetopterus was the species most constant in abundance throughout the year, and Streblospio and Polydora were the least persistent (also indicated in Fig. 4).

There was a general, though non-significant trend indicating that total density and numbers of species were lowest in September or November in both 1973 and 1974 (Fig. 4A, B). Crabs and most fish have been feeding on infauna throughout the summer until this time of the year, then either stop feeding or leave the shallow areas. Thus, the decline in density and number of species may have been due to the continual predation on the infauna throughout the summer. In 1974, total density in December was significantly greater than in November, possibly indicating a rapid repopulation of infauna when predators leave, although other explanations are possible. The opportunistic species (Grassle and Grassle 1974) Streblospio benedicti, Polydora ligni, and Mulinia lateralis, followed this trend of a decrease in density concomitant with continued activity of predators, followed by a large increase in density in late fall after predators leave. These three species live very near or at the surface, and are thus very susceptible to predation or to disturbance at the surface of the sediments.

Figure 4. Monthly abundance patterns, 1973-1974, of (A) total macrofaunal density, (B) number of species, and (C-R) the 16 most common species.





1973 Caging Experiments

In 1973, preliminary experiments were conducted to test the effect on the infauna both of exclusion from and confinement of predators within small areas using wire mesh cages. Predators tested for effects on infauna were the blue crab Callinectes sapidus Rathbun and the hogchoker Trinectes maculatus (Bloch and Schneider), a flat-fish. One cage was divided with wire mesh into quadrants and a crab put in some quadrants ("4-crabs" treatment) to test the effect of density of crabs, or intensity of crab predation. Other quadrants were left empty ("empty $\frac{1}{4}$ " treatment) to test the effect of cage size. Since it was suspected that the cages might affect water currents and sedimentation, a cage with a top but only two sides was used. This cage was placed with the two sides perpendicular to the direction of tidal currents, so as to have maximum effect on currents, while the two open sides would allow crabs and fish access to the infauna under the cage. In the course of the experiment, crabs were observed digging within this partially open cage.

Empty cages and cages with crabs were sampled at two time intervals to determine the time course of the response of the infauna. A summary of treatments, dates, and replicates is given in Table 2.

For each experimental period, differences between treatments were tested by a one-way analysis of variance. Parameters tested were total density, number of species per core, and numbers of individuals per core of all species sufficiently abundant to suspect any significant differences.

TABLE 2

1973 experiments. The number of samples of each replicate treatment at each sampling date. The entry "5 + 5" indicates five cores sampled from each of two replicates.

Treatment	At start of experiment (7-31-73)	After 2½ weeks (8-17-73)	After 2 months (9-29-73)
Uncaged area	5 + 5	5	5 + 5
Empty cage		5	5 + 5
Empty quadrant of cage			5
Cage with Hogchoker			5 + 5
Cage with crab		5	5 + 5
Cage with crab in each quadrant		3	5 + 5
Cage with 2 sides			5

Results after 2½ weeks

On 17 August 1973, after the cages had been in place 2½ weeks, there were few significant differences between any of the treatments sampled. Although there was less than half the total density in the 4-crabs treatment, none of the differences was significant at $\alpha = 0.05$. The number of species per core in the empty cage was significantly greater than all other treatments, and was highly significantly less ($\alpha < 0.01$) in the 4-crabs treatment than any other treatment. Of the species with sufficient density to test statistically, only the chaetopterid polychaete Spiochaetopterus oculatus showed any significant differences between treatments, the 4-crabs treatment having significantly fewer individuals per core than any other treatment and uncaged August samples having more individuals than all other treatments except the empty cage. There were no significant differences between treatments for any other species.

Apparently the number of species per core is a parameter which responds more quickly to the treatments tested. This response was due to the rarer species being eliminated from the cage with four crabs, and increasing in the empty cage. A relatively small change in density of a rare species may be sufficient to affect its probability of being sampled.

The ranks of treatments averaged over both composite parameters and all species tested fall in the following order (top ranked to lowest ranked): empty cage, uncaged at start, uncaged at end, crab, 4-crabs. Species diversity (Shannon H' , Pielou 1966) decreased from 3.63 to 3.15 bits/individual in this ordering, which might also be considered an ordering of treatments from low to high disturbance, thus supporting

the hypothesis that high stress causes low diversity (Sanders, 1968).

Results after 2 months

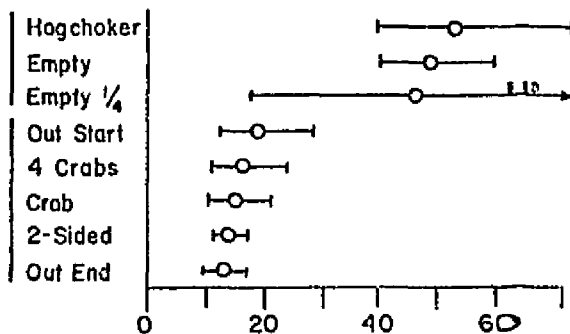
On 29 September 1973, after the cages had been in place 2 months, there were many more significant differences between treatments than after only 2½ weeks. Total density, number of species per core, and number of individuals per core of six species were significantly greater in the empty cage than in either of the cages with crabs (Fig. 5). These six species were Paraprionospio pinnata, Spiochaetopterus oculatus, Streblospio benedicti, Scoloplos robustus, Mulinia lateralis, and Edwardsia elegans. Of these six species, Streblospio and Mulinia are two of the three species shown above to best follow the seasonal pattern of decreasing density coinciding with presence of predators, and are indeed subject to control by crab predation (the third species, Polydora ligni, was present only in cages that were empty or contained a hogchoker, but were not abundant enough to test statistically.

Of the 12 most abundant species, only Phoronis psammophila did not show any significant differences between any of the treatments. Phoronis has a vertical rigid tube which extends deep enough into the sediment (10 cm) to possibly escape predation by crabs. Also showing few significant differences between treatments were Peloscolex gabriellae, Heteromastus filiformis, and Mya arenaria, all of which live or can retract rather deeply into the sediment -- and could thus avoid predation and surface disturbances.

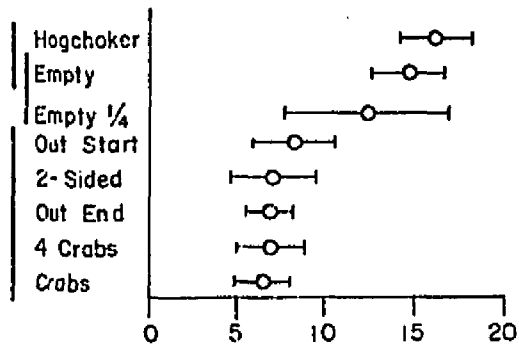
Both total density and number of species per core were highly significantly greater in empty cages, empty ¼ cages, and cages with a hogchoker than in any other treatments, there being an average of

Figure 5. July to September 1973 experiment. Mean and 95% confidence limits ($\bar{X} \pm t_{.05} S_{\bar{X}}$) of total macrofaunal density (A), number of species (B), and density of abundant species (C-N). A, C, D, F-I, K, and N were $\log(x+1)$ transformed; retransformed means and confidence limits are presented. A heavy vertical line extending between two treatments indicates a non-significant ($\alpha = 0.05$) difference between means.

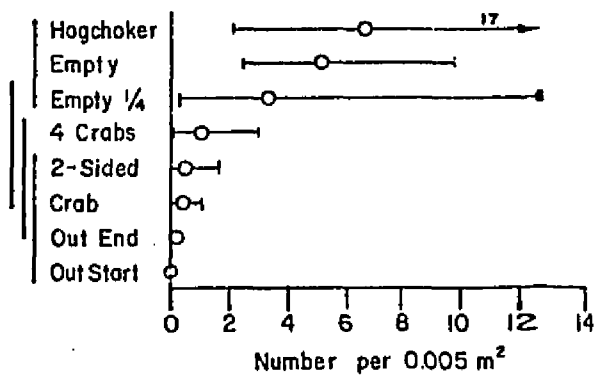
A Total Density



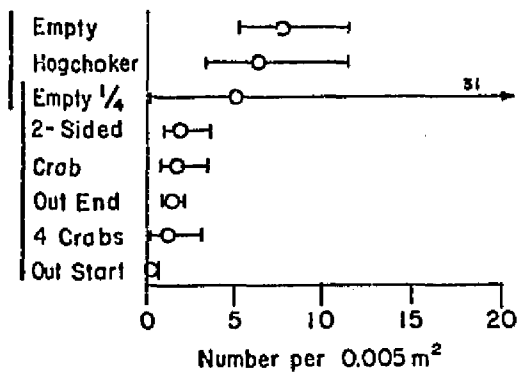
B Number of Species



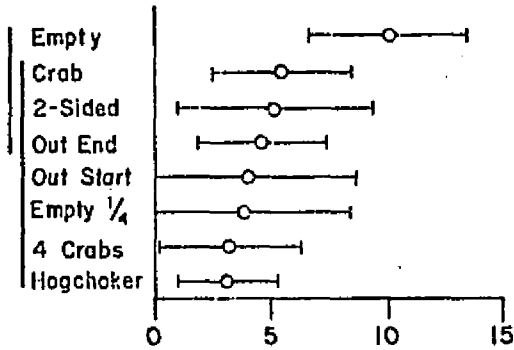
C *Streblospio benedicti*



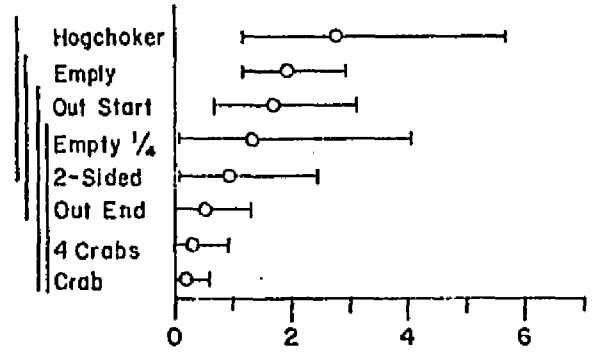
D *Paraprionospio pinnata*



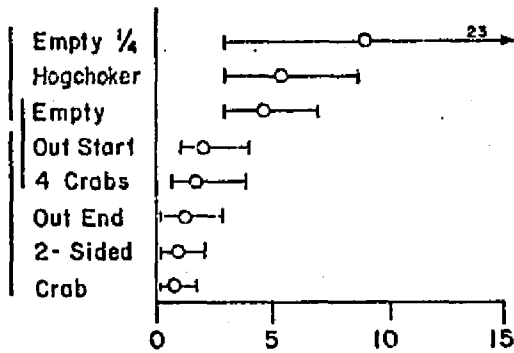
E *Pelosclex gabiellae*



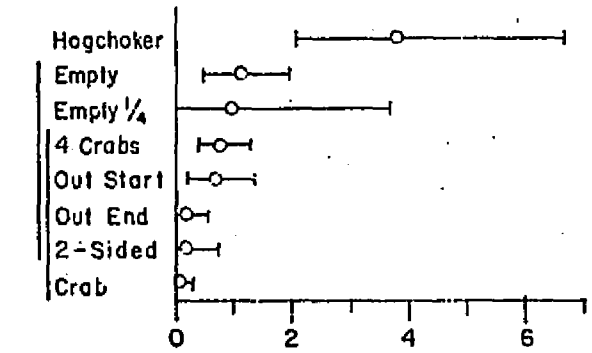
F *Heteromastus filiformis*



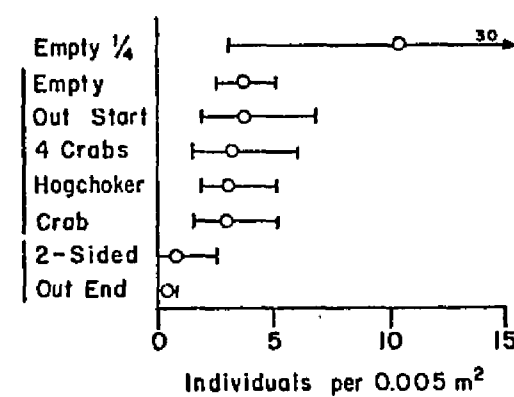
G *Spiochaetopterus oculatus*



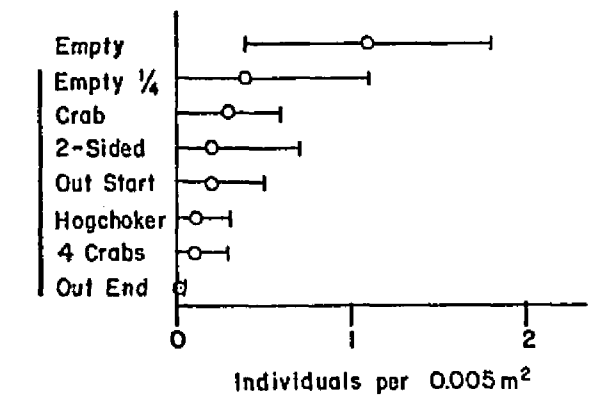
H *Nereis succinea*



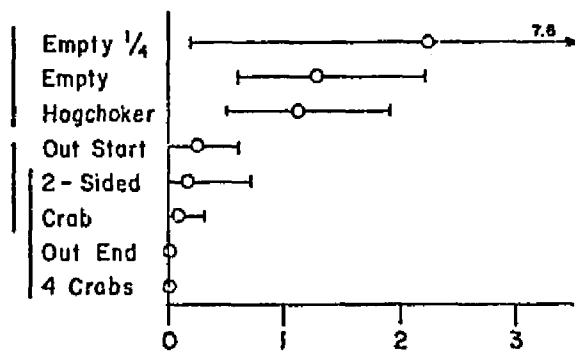
I *Glycinde solitaria*



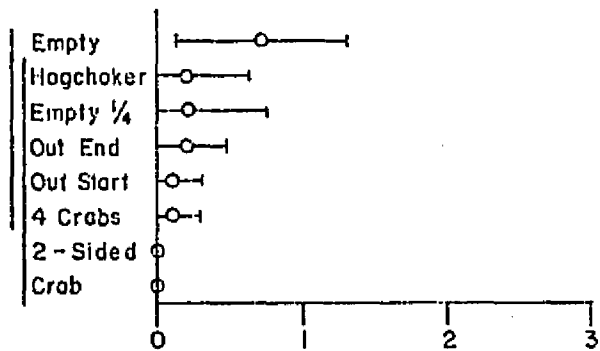
J *Scoloplos robustus*



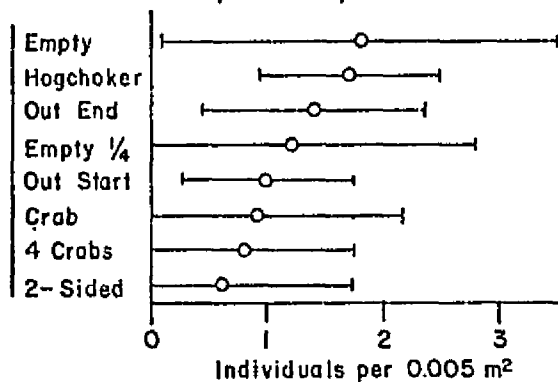
K *Mulinia lateralis*



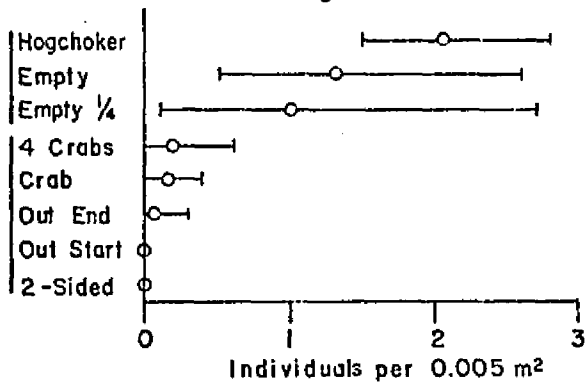
L *Mya arenaria*



M *Phoronis psammophila*



N *Edwardsia elegans*



over three times the total density and twice as many species per core (Fig. 5A, B). These three treatments resulted in similar responses (although all were not significant) in the densities of seven of the 12 species tested: Paraprionospio pinnata, Streblospio benedicti, Spiochaetopterus oculatus, Nereis succinea, Mulinia lateralis, Mya arenaria, and Edwardsia elegans.

There was a general pattern of greater density of most species in empty cages, with the hogchoker treatment producing the same results as an empty cage (Fig. 5). Thus hogchokers (Trinectes maculatus) had little or no controlling influence on the infauna. Both hogchokers used survived the 2 months in the cages, but lost an average of 15% of their body weight over this period. They are abundant (Dovel, Mihursky, and McErlean, 1969) nocturnal feeders (Castagna, 1955), and may feed on animals such as mysids and cumaceans, which are more epifaunal than infaunal, although mainly annelids were found in hogchoker stomachs by Castagna and by Hildebrand and Schroeder (1928). Captivity may have inhibited feeding behavior and caused this discrepancy. Hogchokers are more abundant on mud than sand bottoms, although they were often observed in the study area.

The cages with crabs had essentially the same infauna as the two-sided cage and uncaged areas, implying that natural areas are as disturbed or as preyed upon as an area in which there was a caged crab. Densities in the two-sided cage were generally not significantly different from uncaged areas or cages with crabs, but were significantly less than empty cages, implying that the main effect of the cage was exclusion or inclusion of crabs, and that results were not due in some way to the physical presence of the cage.

The ranks of treatments were averaged over all the species and parameters tested in Fig. 5, and arranged from highest rank (highest density) to lowest rank: empty cage, cage with hogchoker, empty $\frac{1}{4}$ cage, uncaged area at start of experiment, two-sided cage, uncaged area at end, cage with crab, and cage with four crabs (Table 3). As in the August experiment, this ordering might be considered as ranking the treatments from low to high disturbance. Species diversity (Shannon H') generally followed the same pattern, averaging 3.54 bits/individual for the first three treatments, and 3.04 for the latter five treatments.

1974 Caging Experiments

Based on results of 1973 experiments, similar experiments were set up in 1974, but were revised in the following ways. Experiments were started in the spring (May) when more species were spawning, and before blue crabs became abundant. Enough empty cages were put in at this time for sampling at regular intervals. Since the hogchoker apparently did not prey on the infauna, it was replaced by the spot (Sciaenidae: Leiostomus xanthurus Lacépède), known to prey on infauna (Chao, personal communication, Hildebrand and Schroeder 1928, Stickney et al. 1975), dominant in this area (Illowsky and Colvocoresses 1975, Pacheco 1962a, b) and observed feeding in the experimental area. To further test the effect of different crab densities, crabs in three different sized cages were used: a 1 m² cage with a crab ("crab/m²" treatment), a standard size cage (0.5 m square = 0.25 m²) with a crab ("crab" treatment), and a standard size cage divided by wire mesh into quadrants with a crab in each quadrant ("4-crabs" treatment). Thus,

TABLE 3

July to September, 1973, experiment. Frequency of rank of each treatment, based on rank of abundance of total density, number of species, and the 12 most abundant species. All vertical columns do not add up to 14 due to ties in rank.

Treatment	Rank								Average Rank
	1	2	3	4	5	6	7	8	
Empty	5	8	1						1.7
Hogchoker	6	3	2		1	1		1	2.6
Empty $\frac{1}{4}$	3	2	6	2		1			2.8
Out Start			2	4	5		2	1	4.9
2-Sided			1	2	4		6	1	5.8
Out End			1	2		6	2	3	6.1
Crab		1	1		2	5	1	4	6.1
4-Crabs				3	3	1	6	1	6.1

the effective crab densities were $1/m^2$, $4/m^2$, $16/m^2$, respectively. To test the effect of confining a crab to a small area without the presence of a cage, a crab was tethered to a buried stake by a cord attached to a wire looped around the points of the crab's carapace. The 28 cm tether allowed the crab to roam over the same area as a cage ($0.25 m^2$). These crabs fought to escape the tether, appeared to be more active than the crabs in cages, and averaged either one escape or death per month. Tethered crabs and crabs in cages were replaced as soon as they were found to be dead or missing.

An attempt was made to differentiate the effects of crabs caused by: (i) the actual eating of infaunal animals, and (ii) physical burying, crushing, and tube or burrow disruption caused by digging activities associated with feeding and protective burrowing. To make this distinction, I tried to duplicate the physical disturbances caused by a crab. Every 4-5 days the top 2-3 cm of sediment was disturbed and fairly well mixed by reaching through the trap door opening of a cage and walking my fingers heavily through the sediment (as in mixing biscuit dough) and by pushing my fist into the sediment (to simulate the activities of crabs digging for food and burrowing), referred to as the "hand" treatment. A summary of 1974 treatments, dates, and replicates is given in Table 4.

Results after 2 months

On 18 July 1974, after cages had been in place 2 months, composite parameters and most dominant species showed some significant differences between treatments (Fig. 6). Both total density and number of species per core followed the same pattern -- the empty cage,

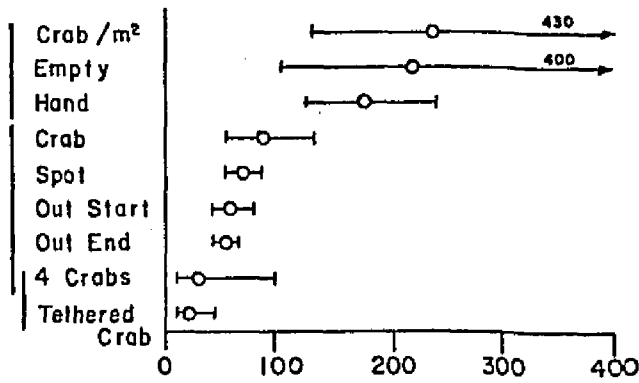
TABLE 4

1974 experiments. The number of samples of each replicate treatment at each sampling date. The entry "5+5" indicates five cores sampled from each of two replicates.

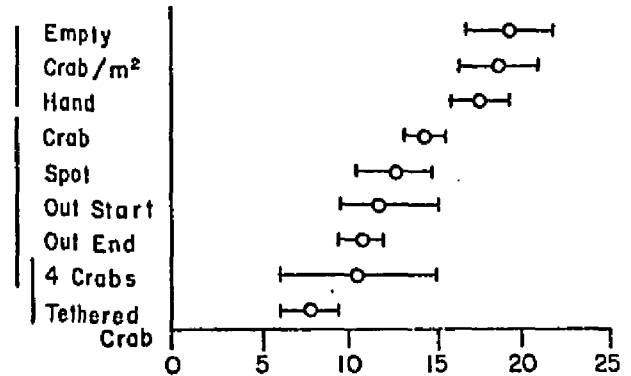
Date (and number of months cages were in)	Empty,		Crab	Crab/m ²	4-Crabs	Tethered crab	Spot	Hand
	Uncaged	then crab						
5-17-74 (6)	5+5	5+5						
7-18-74 (2)	5+5	5+5	5+5	5+5	5	5+5	5+5	5+5
9-18-74 (4)	5+5	5	5					
11-16-74 (1)	5+5	5						
" (6)	5+5	5+5						
" (12)	5+5	5						

Figure 6. May to July 1974 experiment. Mean and 95% confidence limits ($\bar{X} \pm t_{.05} S_{\bar{x}}$) of total macrofaunal density (A), number of species (B), and density of abundant species (C-P). All but B were log (x+1) transformed; retransformed means and confidence limits are presented. A heavy vertical line extending between two treatments indicates a non-significant ($\alpha = 0.05$) difference between means.

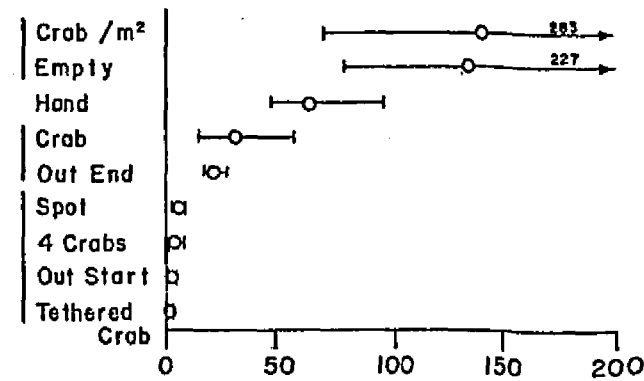
A Total Density



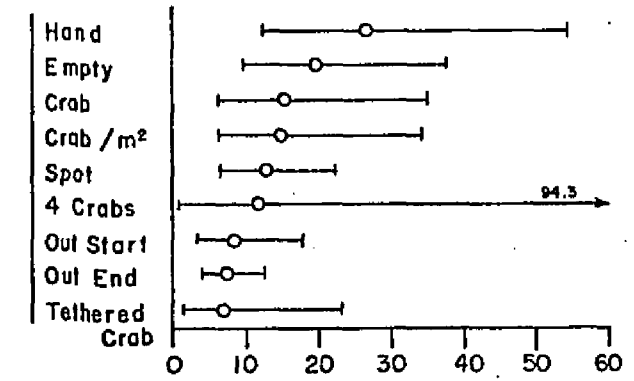
B Number of Species



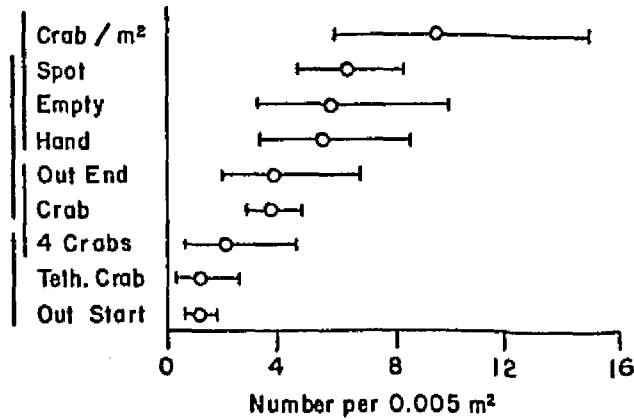
C *Heteromastus filiformis*



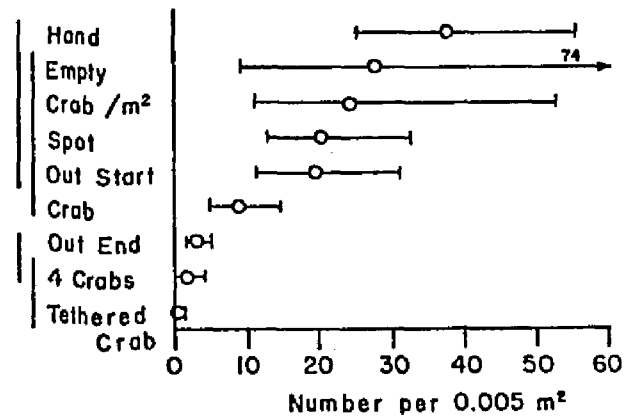
D *Peloscolex gabriellae*



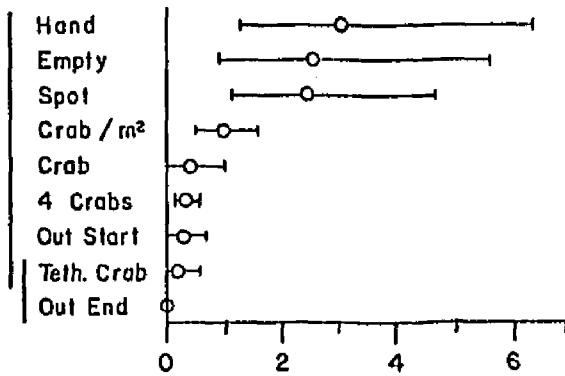
E *Glycinde solitaria*



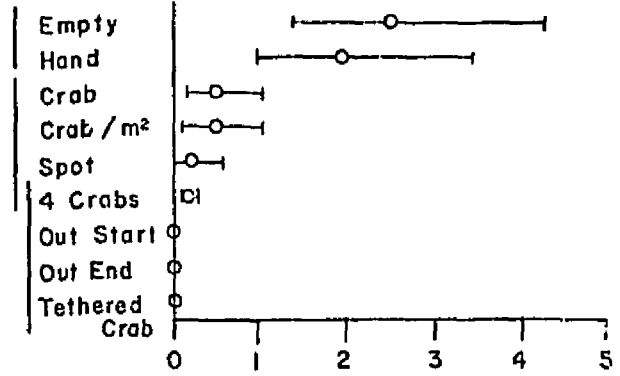
F *Streblospio benedicti*



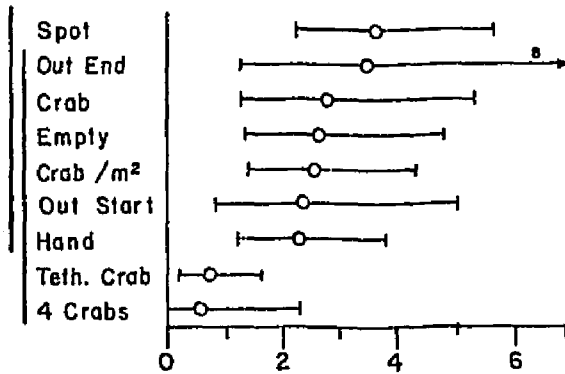
G *Polydora ligni*



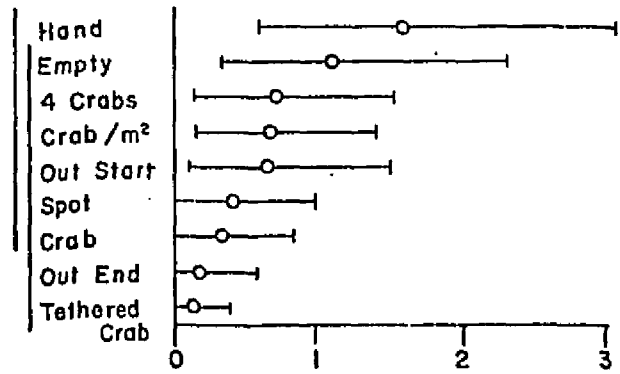
H *Pectinaria gouldii*



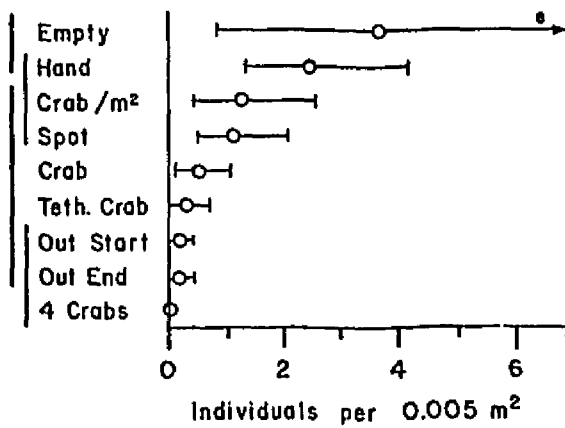
I *Spiochaetopterus oculatus*



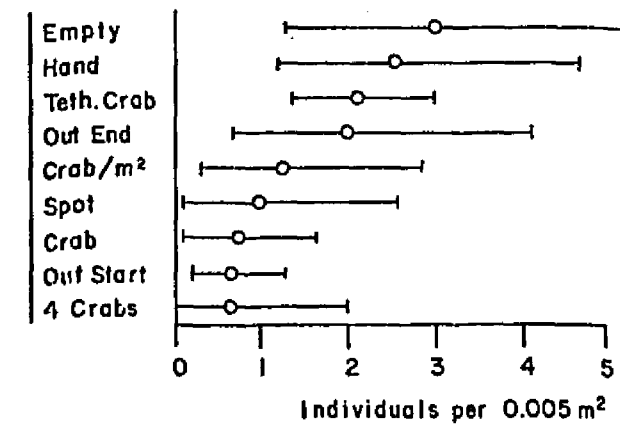
J *Scoloplos robustus*



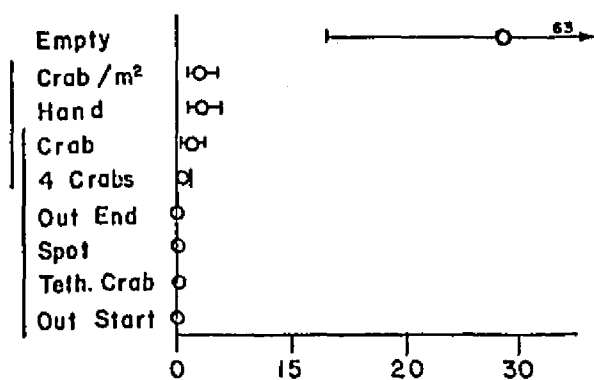
K *Nereis succinea*



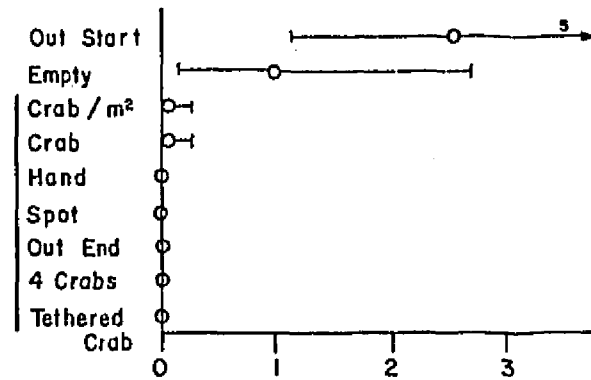
L *Phoronis psammophila*



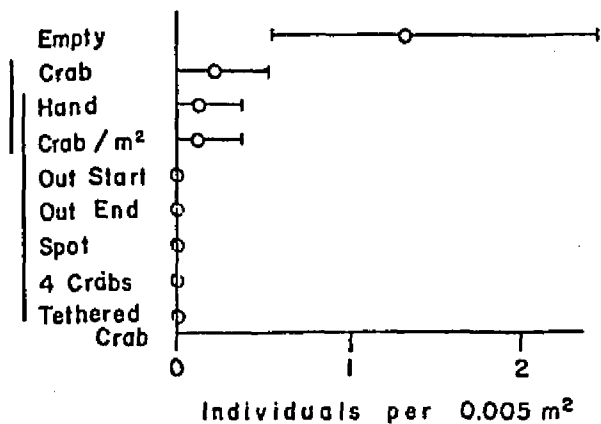
M *Mulinia lateralis*



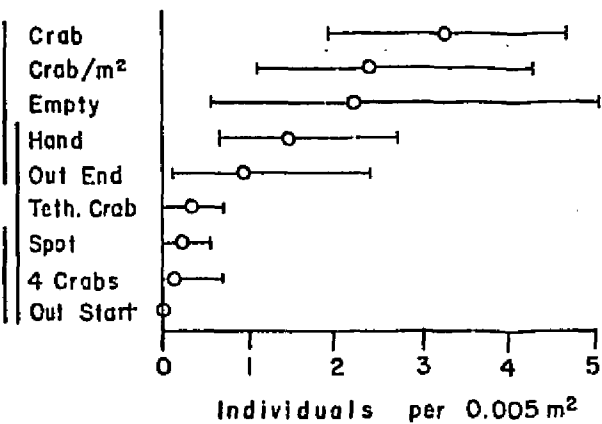
N *Mya arenaria*



O *Lyonsia hyalina*



P *Acteon punctostriatus*



crab/m², and hand treatments were not significantly different from each other, but were all significantly greater than all other treatments. The density and number of species per core were significantly less in the tethered crab treatment than in all other treatments except the cage with four crabs.

Abundances of individual species also followed a pattern similar to 1973. For 12 of the 14 species sufficiently abundant to test statistically, two out of the three treatments with greatest densities were from among the empty, hand, or crab/m² treatments. For 12 of the 14 species, the lowest abundance, excluding that outside the cages at the start of the experiment in May, was either the 4-crabs treatment or the tethered crab treatment. The lowest abundance in nine of these cases was in the tethered crab treatment, but was never significantly less than in the 4-crabs treatment (Fig. 6).

For all species except the bivalves and Heteromastus filiformis, the hand treatment was not significantly different than the empty cage. Thus, the decreases in abundances due to crabs must be due to physical disturbances more severe than the hand treatment, or to actual eating of the infaunal animals, or to a combination of both.

The three species of bivalves, Mya arenaria, Mulinia lateralis, and Lyonsia hyalina, were effectively eliminated by the hand treatment and by any treatments where a crab or fish (spot) was present. Mya was significantly more abundant in uncaged areas at the start of the experiment (May) than in the empty cage in July; otherwise, the densities of all three bivalves were significantly greater in the empty cage than in any other treatment (Fig. 6M, N, O). This difference was highly significant ($\alpha < 0.01$) for Mulinia and Lyonsia, which both live very

close to the sediment surface and thus are available to predators and would be disturbed, buried, or crushed by the hand treatment.

Densities in the crab/m² treatment were greater than the crab treatment (a density of 4 crabs/m²) for nine of the 14 dominant species (two of these differences were significant at $\alpha = 0.05$). Densities in the crab treatment were greater than in the 4-crabs treatment (16 crabs/m²) for all species except Scoloplos robustus (five of these differences were significant). Thus, as blue crab density increases, infaunal densities decrease.

Densities in the tethered crab treatment were less than or equal to those in the 4-crabs treatment for nine of the top 14 species, but were never significantly less. Apparently the increased activity of the tethered crab (noted above) was sufficient to disturb the infauna as much as 16 crabs/m².

The spot (Leiostomus xanthurus) was also effective in reducing infaunal densities. Densities of 12 of the top 14 species were less in the cage with the spot than in an empty cage (seven of these differences were significant). Densities in the spot treatment were intermediate between those in the crab/m² and 4-crabs treatments for 10 of the top 14 species, and intermediate between those in the crab and 4-crabs treatments for seven species (Fig. 6). Thus, the spot was at least as effective as a crab in reducing infaunal densities of most species.

Densities in natural (uncaged) sediments at the time of sampling the cages (July) were intermediate between those of the crab/m² and 4-crabs treatments for seven of the top 14 species, were less than in the crab treatment for 11 of the species (significantly less for

four species), and were greater than in the 4-crabs treatment for seven of the species (Fig. 6). Thus, the infauna of the natural uncaged sediments is at least as disturbed as a caged area with a crab (a density of four crabs/m²).

The ranks of treatments averaged over all species and composite parameters tested in Fig. 6 were arranged from highest rank (highest density) to lowest rank in the following order: empty cage, cage with sediment disturbed by hand, m² cage with crab, cage with crab, cage with spot, uncaged area at end of experiment (July), uncaged at start of experiment (May), cage with four crabs, and the area with a tethered crab (Table 5). As in 1973, this ordering might be considered as ranking the treatments from low to high disturbance. Diversity (H') was only 2.14 bits/individual in the 4-crabs treatment, and averaged 2.78 in the other treatments.

Results after 4 months

On 18 September 1974, after cages had been in place 4 months, the following treatments were sampled (Table 4): an uncaged area, an empty cage, and a cage empty for 2 months but then with a crab in it for the next 2 months ("empty→crab" treatment). Results were very similar to those of July 1974.

The empty cage had significantly greater total density more species, and more individuals per core of most species than any other treatment (Fig. 7). The species which were not significantly more abundant in the empty treatment were the deeper-living species Peloscolex gabriellae, Spiochaetopterus oculatus, Mya arenaria (mean size = 32.7 mm), and Phoronis psammophila. Total density, number of

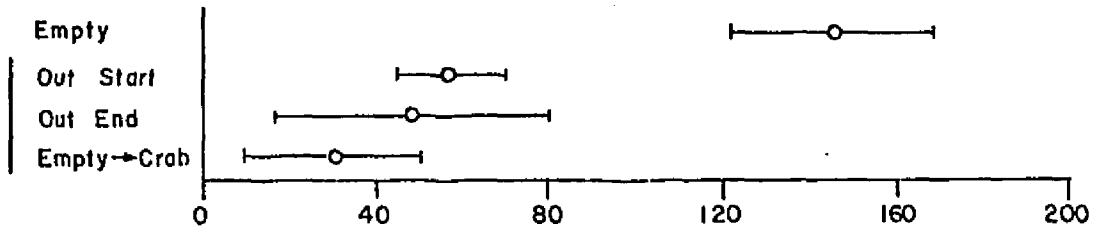
TABLE 5

May to July, 1974, experiment. Frequency of rank of each treatment, based on rank of abundance of total density, number of species, and the 14 most abundant species. All vertical columns do not add up to 16 due to ties in rank.

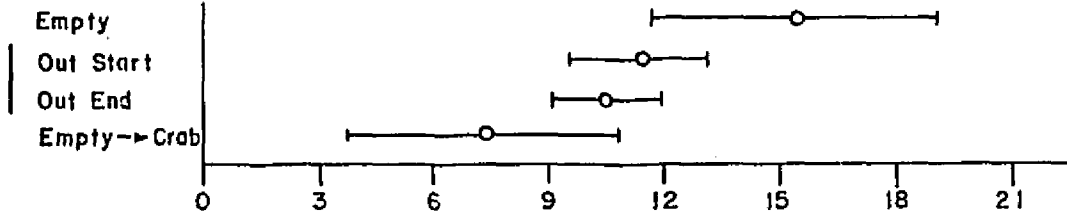
Treatment	Rank									Average Rank
	1	2	3	4	5	6	7	8	9	
Empty	6	7	2	1						1.9
Hand	4	3	5	2	1		1			2.8
Crab/m ²	3	3	3	5	2					3.0
Crab	1	1	3	5	2	2	2			4.3
Spot	1	1	1	2	6	3	2			4.7
Out End		1		1	5	1	4	3	1	6.1
Out Start	1				3	3	4	2	3	6.6
4 Crabs			1		3	3	2	4	3	6.8
Tethered Crab			1		2	2	1	4	6	7.4

Figure 7. May to September 1974 experiment. Mean and 95% confidence limits ($\bar{X} \pm t_{.05} S_{\bar{X}}$) of total macrofaunal density (A), number of species (B), and density of abundant species (C-L). C, D, E, H, and J were log (x+1) transformed; retransformed means and confidence limits are presented. A heavy vertical line extending between two treatments indicates a non-significant ($\alpha = 0.05$) difference between means.

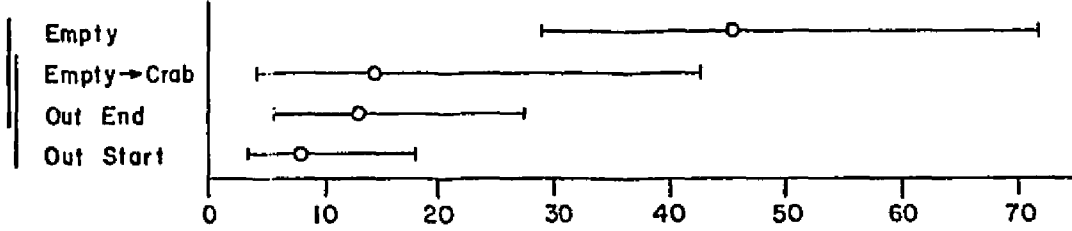
A Total Density



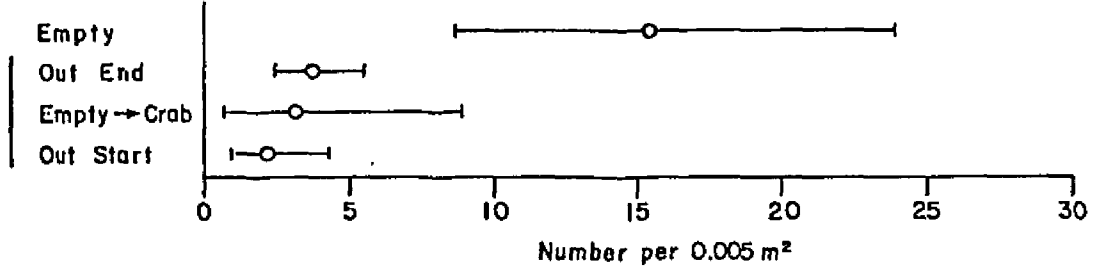
B Number of Species



C *Pelosclex gabriellae*

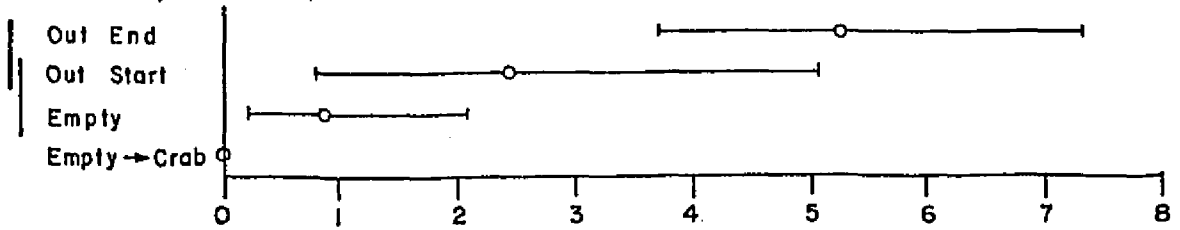


D *Heteromastus filiformis*

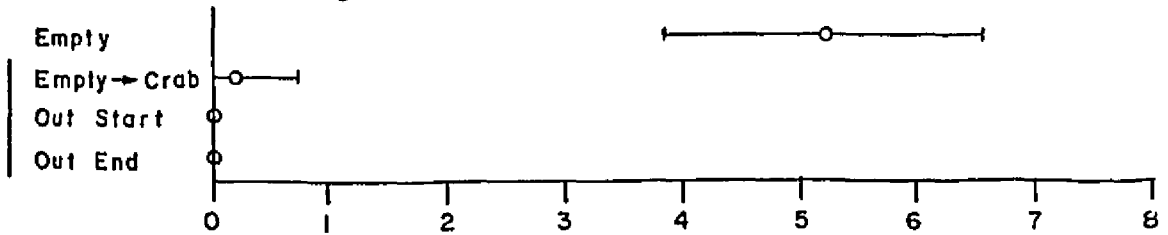


Number per 0.005 m²

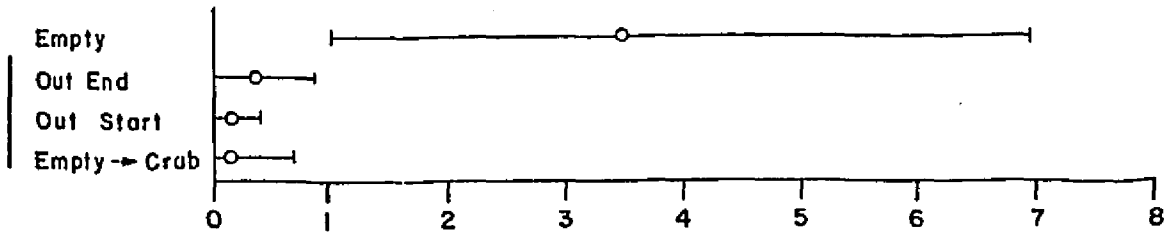
E *Spiochaetopterus oculatus*



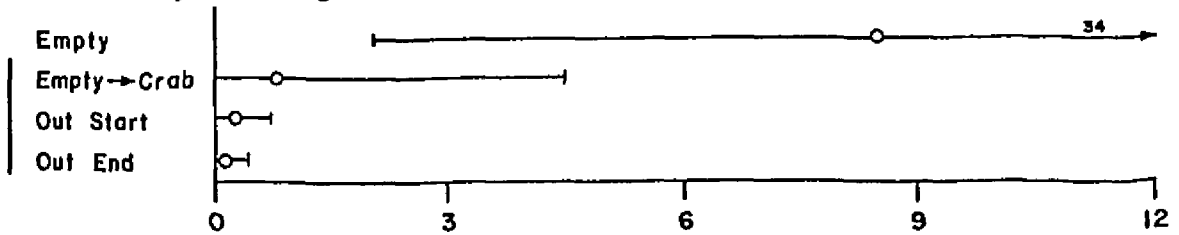
F *Pectinaria gouldii*



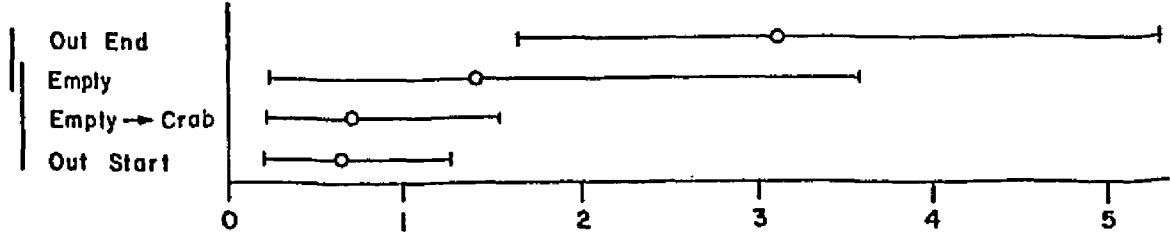
G *Nereis succinea*



H *Polydora ligni*

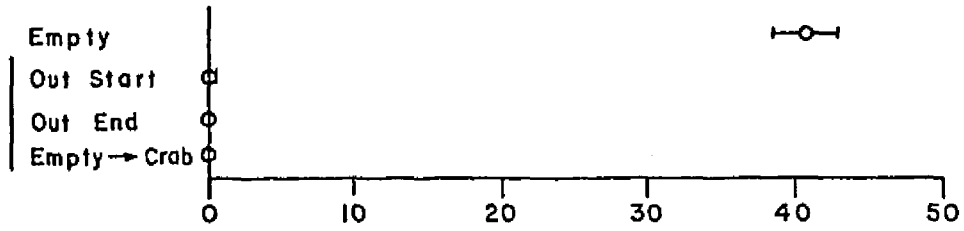


I *Phoronis psammophila*

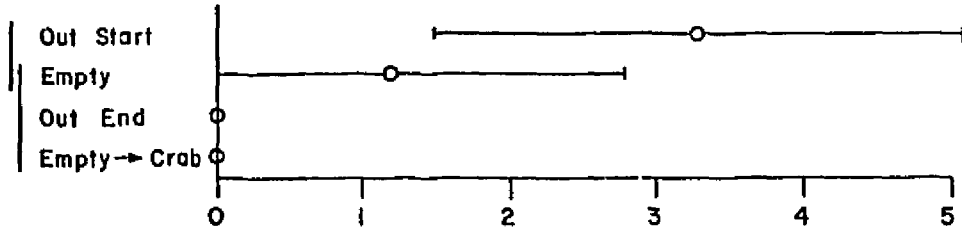


Individuals per 0.005 m²

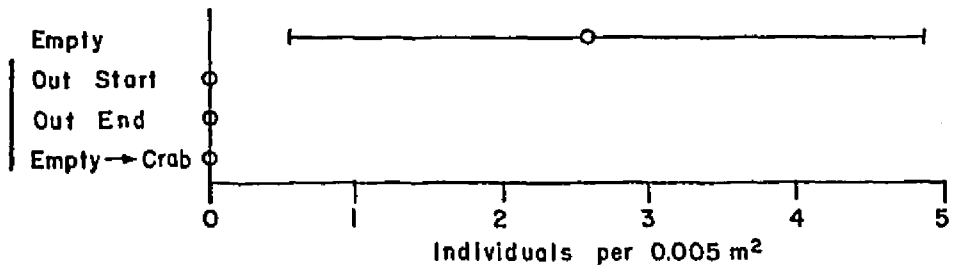
J *Mulinia lateralis*



K *Mya arenaria*



L *Lyonsia hyalina*



Individuals per 0.005 m²

species per core, and densities of half of the species tested were lowest in the empty → crab treatment.

The densities of most species in the uncaged area were more nearly equal to and usually not significantly different from densities in the empty → crab treatment, again indicating that the uncaged natural areas are rather highly disturbed. The ranks of treatments were averaged over all species and composite parameters tested in Fig. 7 and arranged from highest rank (highest abundance) to lowest rank in the following order: empty cage, uncaged area at end of experiment (September), uncaged area at start (May), cage empty for 2 months and then with a crab for 2 months (Table 6).

Results after 6 months

On 16 November 1974 the following treatments were sampled: uncaged areas, empty cages in place for 6 months (since May), an empty cage in place for 1 month, and an empty cage in place for 1 year. The results from cages set out in May will be described first.

The empty cage in place since May (6 months) had highly significantly greater total density and species per core, and significantly greater density of 10 of the 15 species tested than the uncaged areas (Table 7). Species with especially high densities in the empty cage were: Peloscolex gabriellae, Heteromastus filiformis, Pectinaria gouldii, Polydora ligni, Nereis succinea, Mulinia lateralis, and Mya arenaria. All of the above species had also been abundant in empty cages in July (after 2 months) and September (after 4 months), with the exception of Mya in September (Table 7).

TABLE 6

May to September, 1974, experiment. Frequency of rank of each treatment, based on rank of abundance of total density, number of species and the 10 most abundant species. All vertical columns do not add up to 12 due to ties in rank.

Treatment	Rank				Average Rank
	1	2	3	4	
Empty	9	2	1		1.3
Out End	2	3	6	1	2.5
Out Start	1	5	3	3	2.7
Empty→Crab		4	5	4	3.3

Sediments

The cages did affect sediment size and movement. Empty cages, the least disturbed treatment, tended to have a higher percentage (up to 35%) of fine sediments (silts and clays) than physically disturbed sediments (18-19%), or cages with crabs or spot (14-16%), or areas outside cages (11-16%). This increase in fine sediments in the empty cage could be due either to reduction of currents or to increased biodeposition and binding of fine particles by animals such as Streblospio benedicti or Polydora ligni.

Orange-painted sand placed outside the cages was noticeably dispersed in the direction of tidal currents within a few hours, whereas inside the cages this sediment did not move for at least 7 days. Part of this effect may have been due to increased binding of sediments by the greater density of animals in the cages. However, on one occasion in November when painted sand was put out, within a few hours it was covered over and stabilized by diatoms, mainly Nitzschia closterium, both inside and outside cages (see Holland et al. 1974).

The Empty Cage : General Results

The general pattern of results from the empty cage treatment is presented here; individual species patterns will be presented below. The empty cage resulted in increased densities of most species, but the specific results depended on a number of factors.

The length of time a cage had been in place determined whether there were any significant differences in density between the infauna in an empty cage and in an uncaged area. After 2½ weeks in 1973, there were no significant differences for any of the species.

After 2 months, densities of seven species were significantly greater in the empty cage than in an uncaged area (Fig. 5). In 1974, after 1 month there were only two species with significantly greater densities in the empty cage; after 2, 4, 6, and 12 months, there were 8, 6, 9 and 9 species, respectively, that had significantly greater densities in the empty cage than in an uncaged area (Figs. 6, 7; Table 7). Thus, few significant differences occur in 1 month or less, but many significant differences occur after 2 months. Leaving the cage in longer than 2 months did not, however, appreciably change the results. Essentially the same species were more abundant after 2, 4, or 6 months. It is possible that density-dependent regulation of these populations prevented further increases after 2 months. Number of species per core, total density, and diversity did not change much from 2 to 6 months, indicating that succession was not taking place after 2 months (Fig. 8).

The season when a cage was set out determined which species increased in abundance in the empty cage. Recruitment into empty cages was predominantly by larvae rather than by adults, a finding based on sizes of individuals. Thus, if, during the time the cage was in place, the larvae of species A were in the plankton and ready to set, but those of species B were not, species A would increase in abundance in the empty cage and species B would not. A summary of results of empty cages set out at various times and left for various lengths of time is presented in Table 7. In general, any empty cage left for 2 months or longer had significantly greater total density, more species per core, and more individuals per core of most species than there were outside the cages in natural uncaged sediment.

TABLE 7

Average density per core (No./0.005 m²) in empty cages set out at different dates and left in place for different lengths of time.

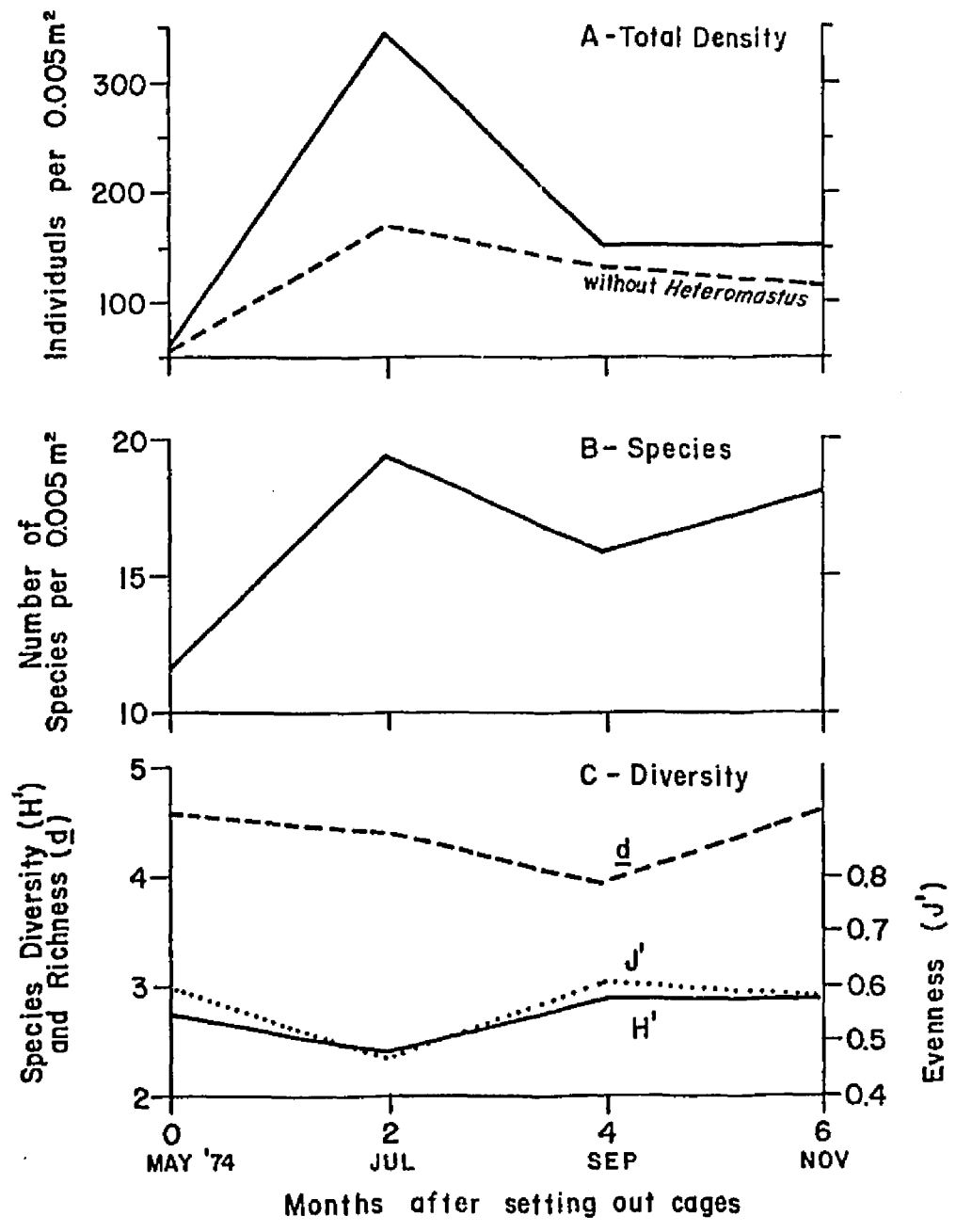
Species or Parameter	Date set out and date sampled (number of months in place)										Average outside 1974
	July- Aug 73 (0.3)	July- Sept 73 (2)	Nov 73- May 74 (6)	Nov 73- Nov 74 (12)	May- July 74 (2)	May- Sept 74 (4)	May- Nov 74 (6)	Oct- Nov 74 (1)	April- July 75* (3)	April- July 75* (3)	
Total density	22.4	51.6	1202.8	159.0	344.2	145.8	150.1	53.6	143	55.4	
Number of species	10.0	14.8	24.2	20.0	19.3	15.4	18.3	15.4	20.0	11.6	
<u>Beloscolex gabriellae</u>	3.2	10.1	24.2	27.4	57.6	48.0	53.3	15.6	0	20.5	
<u>Heteromastus filiformis</u>	4.5	2.2	17.6	42.2	60.9	15.4	35.7	2.4	15.0	7.3	
<u>Spiochaetopterus oculatus</u>	3.0	5.1	2.2	2.6	3.5	1.0	2.8	3.8	3.0	4.6	
<u>Streblospio benedicti</u>	0	7.2	720.0	12.0	52.4	0.2	3.5	11.4	40.0	6.0	
<u>Glycinde solitaria</u>	2.2	4.0	2.4	3.0	7.7	1.4	1.9	2.0	3.0	1.8	
<u>Polydora ligni</u>	0	0.3	23.0	16.4	4.1	12.6	3.8	1.2	43.0	2.3	
<u>Paraprionospio pinnata</u>	0.4	8.6	0.8	1.2	0.1	0	0.5	1.4	0	0.9	
<u>Scoloplos robustus</u>	0	1.1	1.6	7.8	0.3	0	1.2	4.4	3.0	0.6	
<u>Eteone heteropoda</u>	0	0.4	18.6	2.0	0.5	0	1.7	0.1	1.0	0.5	
<u>Nereis succinea</u>	0.8	1.3	1.8	6.2	4.5	3.8	5.8	0	7.0	0.6	

TABLE 7 (Continued)

Species or Parameter	Date set out and date sampled (number of months in place)												Average outside cages in 1974
	July- Aug 73	July- Sept 73	Nov 73- May 74	Nov 73- Nov 74	May- July 74	May- Sept 74	May- Nov 74	May- Nov 74	Oct- Nov 74	April July 75*			
	(0.3)	(2)	(6)	(12)	(2)	(4)	(6)	(6)	(1)	(3)	(3)		
<u>Pectinaria gouldii</u>	0.2	0.6	0	0.4	1.7	5.2	3.5	0	4.0	0.01			
<u>Glycera dibranchiata</u>	0.2	0.3	10.0	0.1	0.1	0	0	0.6	0	0.5			
<u>Mulinia lateralis</u>	1.2	1.5	19.2	4.2	44.1	41.0	20.3	0.2	3.0	0.1			
<u>Mya arenaria</u>	0	0.7	336.2	15.8	2.0	1.2	4.2	0.8	4.0	0.4			
<u>Lyonsia hyalina</u>	0	0	3.2	0	1.6	2.6	0.1	0	1.0	0.00			
<u>Acteon punctostriatus</u>	0	0.1	0.2	0.8	3.8	0	0	0	2.0	0.5			
<u>Nassarius vibex</u>	0	0.8	0.2	0.3	0.5	0	1.4	0	0	0.04			
<u>Phoronis psammophila</u>	1.6	1.8	1.4	1.6	4.4	1.6	1.4	2.0	3.0	2.2			

*Only one core processed.

Figure 8. Community parameters of infauna versus time in exclosures (A) total density, (B) number of species, and (C) diversity (H'), richness ($\underline{d} = S - 1/\ln N$), and evenness ($J' = H'/\log_2 S$) components, where $S =$ number of species.



Individual Species Patterns

Peloscolex gabriellae Marcus

The tubificid oligochaete Peloscolex gabriellae, which lives in a vertical burrow with its posterior end sticking above the sediment surface, feeds at the bottom of its burrow which may be 5 cm or more deep and ejects its fecal pellets in a mound at the surface. This species broods its young, which develop directly, and has a highly clumped spatial distribution (average variance-to-mean ratio = 8). There is no distinct seasonal pattern of abundance (Fig. 4C); perhaps the species breeds over a period of many months. Probably due to its deep-dwelling habit, its ability to retract very quickly into its burrow, and its mode of reproduction, Peloscolex gabriellae showed relatively small increases in empty cages (Table 7), was relatively unaffected by crabs in cages (Figs. 5G, 6I, 7E), and showed no significant differences in abundance at crab densities of 0, 1, 4, or 16 crabs/m² (Fig. 6D). Thus, by a rapid avoidance reaction, Peloscolex gabriellae avoids predators, and its abundance is not controlled by predation, which may in part explain why Peloscolex is the most abundant species in the natural community.

Heteromastus filiformis (Claparede)

The capitellid polychaete Heteromastus filiformis lives in a mucus-lined burrow and is similar in living and feeding habit to Peloscolex gabriellae. Heteromastus, and opportunistic species with planktonic larvae, was variable in abundance (Fig. 4D, Table 1), and was able to recruit heavily into empty cages. For example, in two of the cages set out in May and sampled in July 1974, one replicate each

of the empty and crab/m² treatments had Heteromastus densities of over 51,000/m².

In the natural uncaged sediment, Heteromastus had a peak abundance in summer, 1974. In any empty cage that was out during this period (May to July, May to September, May to November, and November 1973 to November 1974), Heteromastus density increased significantly over the density in uncaged sediments.

Spiochaetopterus oculatus (Gitay)

The chaetopterid polychaete Spiochaetopterus oculatus lives in a vertical chitinous tube which often protrudes above the sediment surface and extends 10-15 cm into the sediment. Spiochaetopterus was observed, both in the laboratory and the field, to feed on surface deposits within a radius up to 10 cm with its paired tentaculate palps, moving the food particles along ciliated grooves, in contrast to primarily suspension feeding as reported by Barnes (1964).

As measured by an index of persistence, Spiochaetopterus had the least fluctuating abundance of any of the dominant species (Table 1, Fig. 4E). Embryos brooded in tubes were observed from May to September, and juveniles were present in samples from uncaged areas from June to November, with the most juveniles present (42-46% of total) in samples from August through October.

Spiochaetopterus did not increase in abundance in empty cages as much as many other species, and was significantly reduced in abundance by predation by crabs but not by fishes. The fishes, particularly the hogchokers, were not able to forage as deeply into the sediment as the crabs.

Streblospio benedicti Webster

The spionid polychaete Streblospio benedicti feeds in much the same manner as Spiochaetopterus, feeding on surface deposits with long peristomial palps. Its fragile membranous-and-mud tubes help to bind together the top 1-2 cm of surface sediments. In the empty cage in place from November 1973 to May 1974, Streblospio was extremely dense (140,000/m²). Its short, approximately vertical tubes bound the surface sediments together in a mat so well that the top 2 cm of sediment could be carefully picked up intact. Perhaps it was this sediment stability that allowed the soft clam Mya arenaria to set in this cage in such great density (65,000/m²).

Streblospio exhibits the typical pattern of an opportunistic species (Grassle and Grassle, 1974) whose population fluctuates irregularly (Fig. 4F) and responds to available space (an empty cage) with a large population increase (Table 7). Both juvenile individuals and adults brooding embryos were found in samples from uncaged areas in most months sampled. Juveniles were most abundant in April and May, and gravid individuals were most abundant in May, June, and July (an average of 245/m²).

Streblospio had been very abundant in empty cages set out in May and sampled after 2 months in July 1974 (most were juveniles 2-4 mm long; some were gravid adults 10-12 mm). By September (after 4 months), Streblospio was less abundant in the empty cage than outside cages. Also, in November 1974 (after 6 months), Streblospio density in the empty cage was not significantly different than outside the cages and was less than that in May when the cages were originally set out. Outside the cages, Streblospio density also declined from May to November,

suggesting that this decline is a natural occurrence after spawning, unrelated to crab or fish predation.

Neither of the fish species used was effective in reducing densities of Streblospio. The crab and 4-crab treatments were effective in significantly reducing Streblospio densities below densities in empty cages in both 1973 and 1974 (Figs. 5C, 6F).

Polydora ligni Webster

Another opportunistic spionid polychaete, Polydora ligni feeds on surface deposits in much the same manner as Streblospio benedicti and Spiochaetopterus oculatus mentioned above. The mud tubes of Polydora also help to stabilize the surface sediments. Polydora behaves as an annual or semiannual species in Chesapeake Bay, with peak density in late winter or early spring and very low densities at other times of the year (Fig. 4G, Orth 1971, Boesch 1973, Virnstein 1975).

Even though Polydora abundance was very low during the periods that most cages were set out, abundances increased significantly in nearly all empty cages. However, the largest increases in abundance were in empty cages set out during periods when Polydora larvae were heavily setting (Table 7; Figs. 6G, 7H).

Paraprionospio pinnata (Ehlers)

Another spionid polychaete, Paraprionospio pinnata, was common, but never abundant during the 1960's in mud bottoms in the lower York River, then became a dominant species from 1972-1975 following Tropical Storm Agnes in June 1972 (Boesch, Diaz, Virnstein, in press, Virnstein 1975, Boesch, Wass, Virnstein, in press).

Paraprionospio pinnata was significantly more abundant in empty cages after 2 months in 1973 (Fig. 6D), but was never significantly more abundant in empty cages in 1974 and, in fact, was usually less abundant in empty cages. Densities of Paraprionospio in cages with crabs were significantly less than in empty cages, but were not different than densities in uncaged areas. Thus, Paraprionospio abundance may be controlled by crab predation.

Paraprionospio is an active worm, moving about in its branching burrows. Recruitment into the empty cages in 1973 could have been by adults, based on the large size of the individuals.

Scoelelepis squamata (Muller)

Another spionid polychaete, Scoelelepis squamata, commonly occurred in low densities in most months' samples from uncaged areas in 1974 (Table 1, Fig. 4I), but was never more abundant in any empty cage than outside cages. Thus, Scoelelepis abundance does not seem to be regulated by crab or fish predation. Perhaps Scoelelepis lives deeply enough in the sediments to avoid predation. However, many individuals were found with their guts stuffed with sand grains, foraminiferans, and ostracods--the latter two most abundant at the sediment surface.

Pectinaria gouldii (Verrill)

The pectinariid polychaete Pectinaria gouldii feeds on deposits at the bottom of its inverted cone-shaped tube, and is normally found only in very low densities in uncaged sediments; average density in 1974 was 2/m². Density was significantly greater in empty cages in July and September ($\alpha < 0.001$) and in November ($\alpha < 0.05$) 1974 than in

uncaged areas (Table 7, Figs. 6H, 7F). Crabs and spot were effective in reducing Pectinaria abundance, but the hand treatment was not. Peer (1970) estimated that 80% of Pectinaria hyperborea mortality in St. Margaret's Bay, Nova Scotia was due to fish predation.

In the empty cage in July, most of the Pectinaria were small (2-3 mm long, 0.6 mm opercular plate diameter); in September, most were very large individuals (30-58 mm long, 7 mm opercular plate); in November, individuals were larger still (48-60 mm long, 8 mm opercular plate). Such large individuals are rarely, if ever, found in Chesapeake Bay, the implication being that Pectinaria rarely lives more than a few months in the natural environment (at least during the summer) and that crab and fish predation may be the major factor regulating Pectinaria density.

Glycinde solitaria (Webster)

The goniadid polychaete, Glycinde solitaria, had a relatively uniform density with peaks of abundance in July of both 1973 and 1974 (Table 1, Fig. 4J), when most of the individuals were juveniles (2-3 mm). Glycinde density followed the usual pattern of being greater in empty cages than in cages with crabs in September 1973 and July 1974 (Figs. 5I, 6E). In September and November 1974, there were no significant differences between any of the treatments in spite of continuing recruitment, as indicated by the fact that the majority of individuals in samples from uncaged areas in September and November were juveniles. Glycinde density is thus only moderately controlled by crab predation; the decline after the July peak may be unrelated to crab predation.

Glycera dibranchiata Ehlers

The density of the glycerid polychaete Glycera dibranchiata was normally very low (averaging $54/m^2$) except in May, when the density of juveniles (1.5-4 mm) was $390/m^2$ (Fig. 4K). May was the only month that juveniles were present, except for one 2 mm individual found in February.

The cage in place from November 1973 to May 1974, during the early spring setting of Glycera, had a significantly greater density ($1940/m^2$) than outside the cages (Table 7); most were juveniles 2-3 mm. However, the cage in place from November 1973 to November 1974 had the same low density as that outside the cages ($39/m^2$). Perhaps this decline is due to natural mortality, or the actively burrowing Glycera may have migrated from the empty cage between May and November.

Scoloplos robustus Verrill

Juvenile individuals (1-4 mm) of the orbinid polychaete Scoloplos robustus were found in uncaged areas in December 1973 and August to December 1974, with maximum abundance in December 1974. The peaks in abundance of Scoloplos correspond fairly well to peaks in juvenile abundance, and fluctuations in abundance thus appear to be due partly to fluctuations in larval recruitment.

Scoloplos was significantly more abundant in empty cages only in September 1973 and November 1974 (Fig. 5J, Table 7); almost all of these individuals were juveniles 2-5 mm long. In July, the greater density of Scoloplos in the empty and hand treatments was due to larger individuals 16-40 mm long.

Eteone heteropoda Hartman

The abundance of the phyllodocid polychaete Eteone heteropoda, like Scoloplos, depends on larval recruitment. Juvenile Eteone (1-4 mm) were present in samples from uncaged areas (in order of decreasing abundance) in May, February, December, and June 1974. All peaks in density of Eteone (Fig. 4M) correspond to peaks of juvenile density.

It is thus reasonable that the empty cage in place from November to May, during the recruitment period of Eteone (December to June), had the greatest Eteone density (3600/m², mostly juveniles 2-3 mm long) of any treatment at any time (Table 7). There were also significantly more Eteone in empty cages put out in November 1973 and May 1974 and sampled in November 1974; these periods also included all or part of the recruitment period. There were too few individuals present in any treatment at other major sampling dates (August and September 1973 and July and September 1974) to discern any pattern of response of Eteone to other treatments.

Nereis succinea (Frey and Leuckart)

The peaks in density of the nereid polychaete Nereis (Neanthes) succinea in June and October (Fig. 4N) also corresponded to peaks in density of juveniles. Juveniles were found in samples from uncaged areas from June through December.

All empty cages in place longer than 1 month had a greater density of Nereis (approximately half juveniles) than did uncaged areas (Table 7); most of these differences were significant (Figs. 5H, 6K, 7G). The hogchoker and hand treatments were not effective in reducing Nereis densities, but the crab and spot treatments were (Figs. 6K, 7G).

Phoronis psammophila Cori

The phoronid Phoronis psammophila (= P. architecta Andrews) lives in a rigid vertical tube of sand grains cemented together and suspension feeds with its lophophore. Phoronis was present in samples outside the cages every month (Fig. 4 0); juveniles were present in samples from June through December 1974.

Although recruitment was occurring during periods that cages were in place, none of the empty cages in 1973 or 1974 had significantly greater densities of Phoronis than outside the cages (Table 7, Figs. 5M, 6L, 7I). There was a non-significant trend, however, of greater densities in empty cages and decreasing density with increasing crab and fish predation. Crabs and fish may eliminate some of the smaller individuals, but Phoronis abundance apparently is not significantly regulated by predation.

Mulinia lateralis (Say)

Of all the species collected, the macrid bivalve Mulinia lateralis best exhibits the characteristics of an opportunistic species. Periodic eruptions of very dense populations of Mulinia occur in Chesapeake Bay, particularly in deeper muddy sediments, in winter or early spring (Boesch 1973, Huggett et al. 1975, Boesch 1974, Boesch, Wass, Virnstein, in press), but then experience very high mortalities in early summer, maintaining low-density reservoir populations in shallow sandy areas (Wass et al. 1972). Summer densities were 20/m² in this study area and 37/m² at three 3 m-deep stations in the lower York River from 1972 to 1974 (Virnstein 1975).

Juveniles were found in February, May, June, July, August, September, and November. Additional sampling would likely show that

Mulinia juveniles are present year-round; Chanley and Andrews (1971) found Mulinia larvae in the plankton from May to November.

Young Mulinia can grow very rapidly. At temperatures above 20 C, they grow to sexual maturity in 6 weeks (Calabrese 1969, 1970) at an approximately logarithmic rate that decreases with age (Fig. 9A).

Every empty cage, no matter when set out or sampled, had a greater density of Mulinia than outside cages; most of these differences were significant (Figs. 6-9, Table 7). Mulinia densities in empty cages were highly significantly greater ($\alpha < 0.01$) than in any other treatment on the following dates: November 1973 to May 1974, May to September 1974, May to November 1974, and May 1974 to February 1975.

In those empty cages which remained densely populated with Mulinia, it was probably the increase in size of individual Mulinia (Fig. 9A) which caused overcrowding and a subsequent decline in density (Fig. 9B). The density of the clams was so great that to bury itself, a clam would have to dig through a layer of clams (Figs. 10, 11). By lying on their sides and thrusting their feet out rapidly, clams were observed to "hop" along the sediment surface and thus move laterally. Presumably in response to overcrowding, some clams moved out of the cage in this way. If they moved out during the seasons when crabs were present, these clams were eaten within a few days, as evidenced by the broken Mulinia shells outside the cages.

From the experiments of 1973 (Fig. 5K), it can be seen that Mulinia density is not affected by hogchokers, but is effectively controlled by crab predation. In 1974, crabs and spot were also effective in reducing Mulinia density (Figs. 6M, 7J). As had happened with many other species, the greater the density of crabs, the less the

Figure 9. Mulinia lateralis size versus age (A), density versus age (B), and density versus blue crab density (C).
All are plotted on log scale.

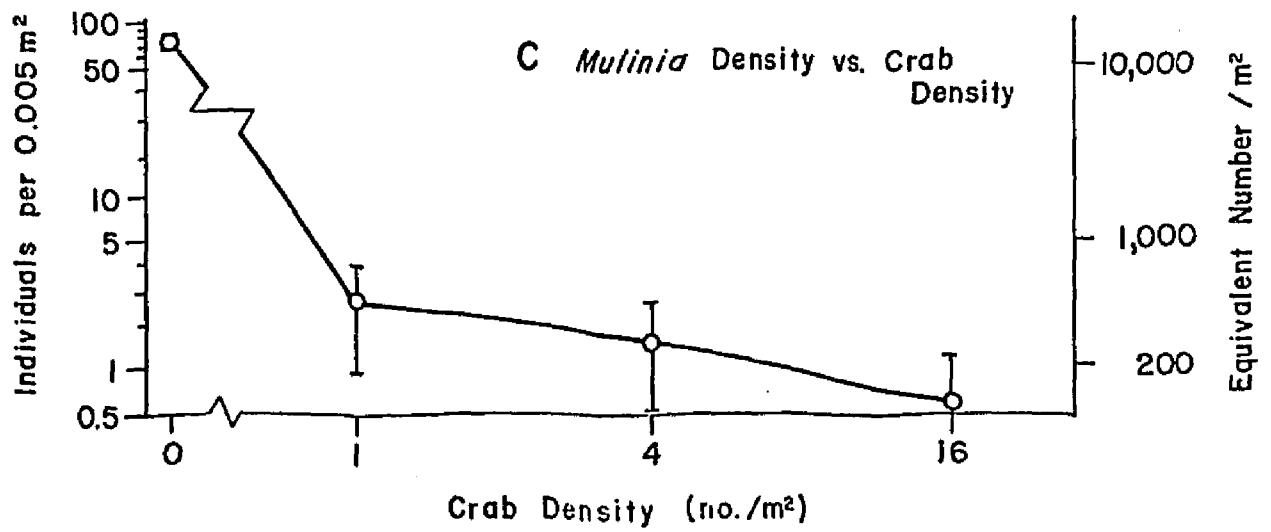
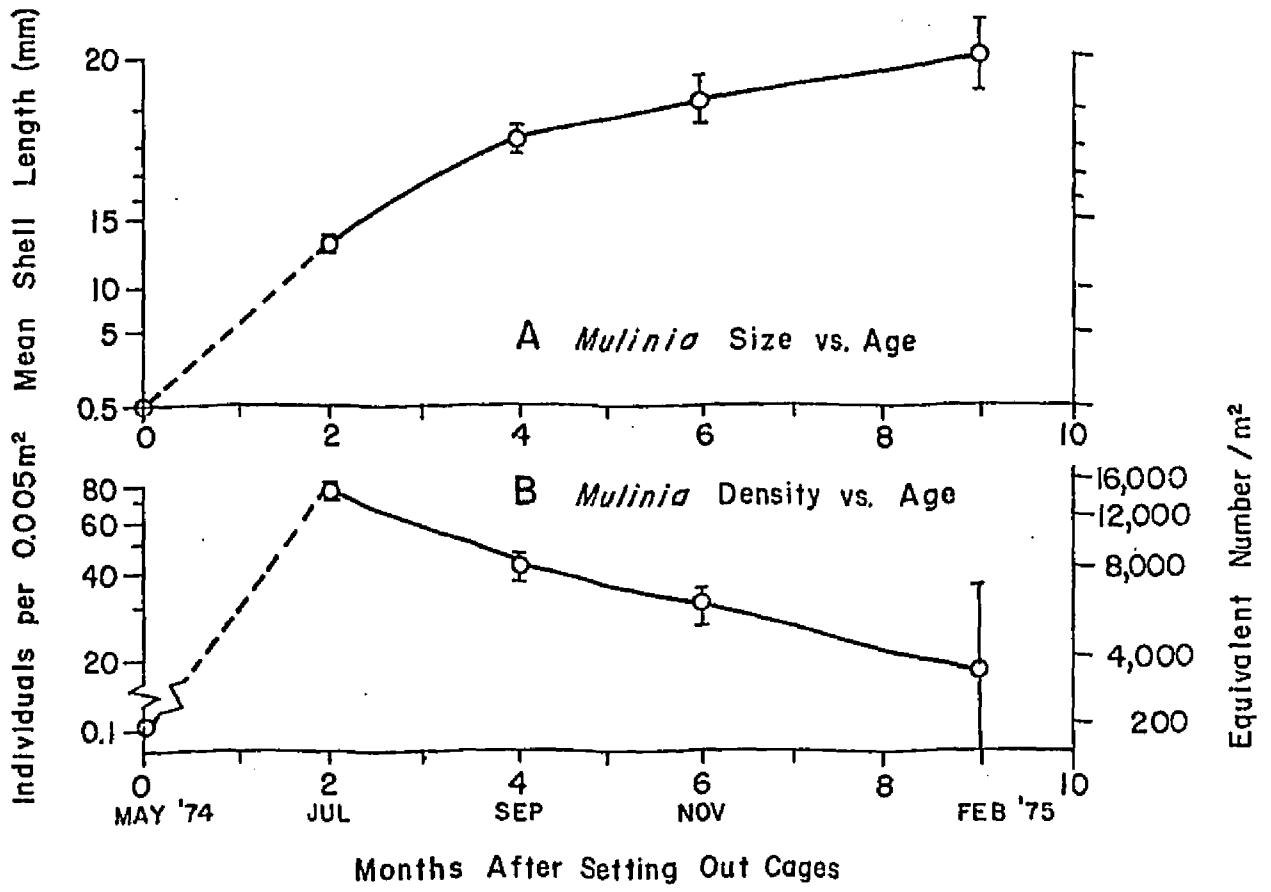
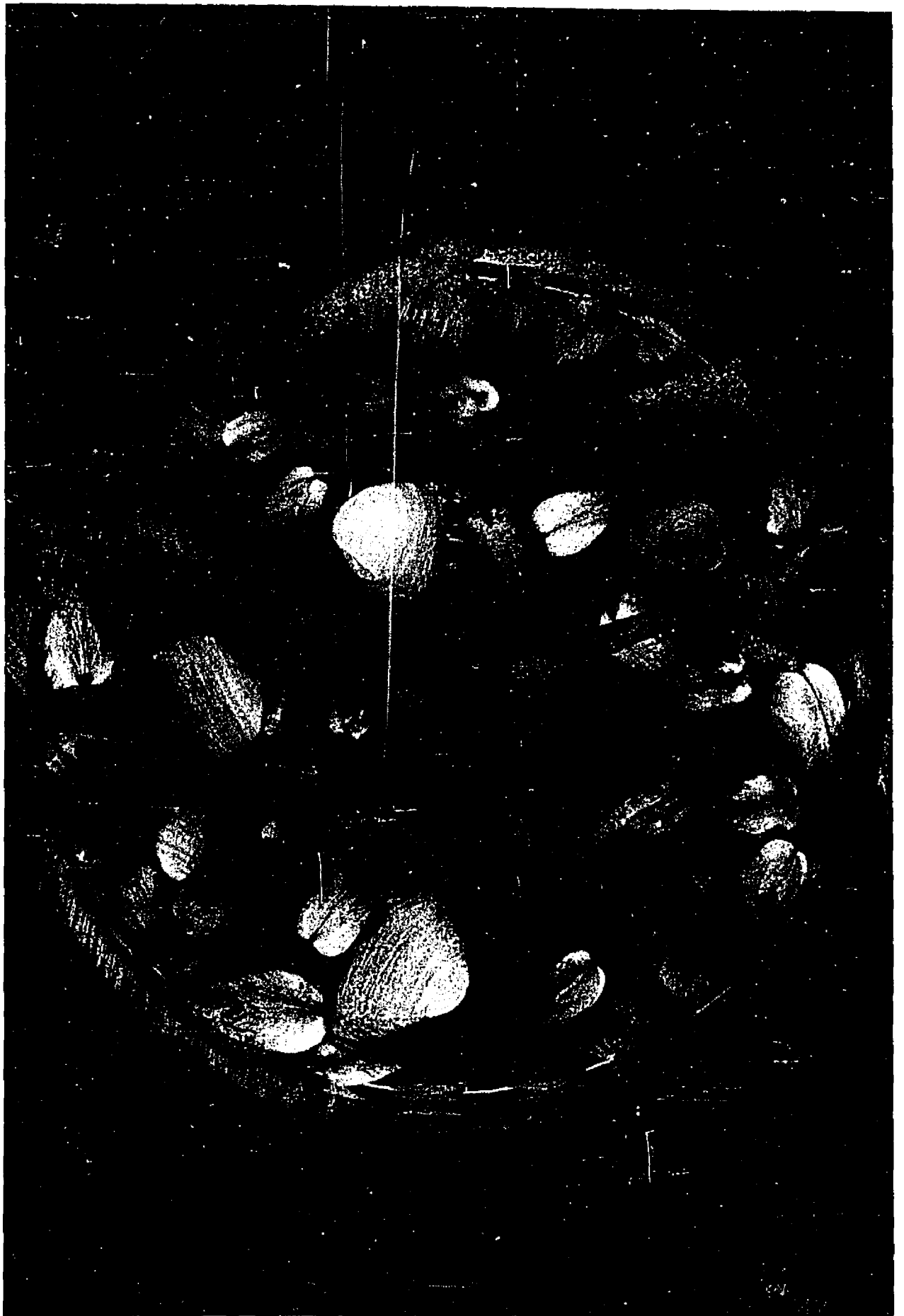


Figure 10. Photograph of undisturbed core taken from enclosure in September 1974, showing Mulinia lateralis and Pectinaria gouldii on the surface, and the numerous siphons of Mulinia. Inside diameter of the core is 10 cm. The animals from this core are pictured in Fig. 11.



Figure 11. Photograph of the animals removed from the core pictured in Fig. 10, consisting of mostly Mulinia lateralis, and some Pectinaria gouldii and Lyonsia hyalina. Diameter of the core is 10 cm; thus the animals are pictured in the actual density from the field.



density of Mulinia (Fig. 9 C). The actual mechanism by which Mulinia populations were kept low may have varied from treatment to treatment. The hand treatments had significantly fewer Mulinia than the empty cages, but significantly more individuals than outside the cages (Fig. 6 M). This manual disturbance of the sediments may eliminate many Mulinia by crushing, burying, or dislodging the newly settled clams from the sediment so that they may be carried away by tidal currents. This hand treatment was less effective than the crabs or spot in eliminating Mulinia. Spot feed mainly in the top few millimeters of sediment (Stickney et al. 1975) and may have eliminated many Mulinia both by actually eating them, and by physical disruption of sediments. By their digging and burrowing, the blue crabs may also have eliminated many Mulinia; in addition, they also were observed to have eliminated a cage full of large Mulinia by eating them.

To verify that blue crabs could actually dig up and eat Mulinia, several large (approximately 18 mm) Mulinia were put into an aquarium containing sediment from the study area and allowed to burrow into the sediment. A blue crab was then put into the aquarium and observed. Two different crabs were used on two different occasions. In both cases, the crabs were observed to find the Mulinia (apparently by chance), dig them up, and eat them. Usually the crab crushed the clams with its chelae, often near the clam's siphon, then proceeded to use its mouthparts to scrape the tissue out of the valves. With two clams, however, the crab was able to get the point of a dactyl of one of its chela between the valves of the clam, did the same with the dactyl of the other chela, and pried open the valves, all in about 15 seconds. The crab then ate the whole clam, even scraping the abductor

muscles off both valves, without breaking either valve of the clam.

There is other evidence that blue crabs eliminated the Mulinia by actually eating them, not just by physically disturbing the sediment. The unplanned but fortuitous empty-crab treatment was a cage that had been empty for 2 months (May to July 1974). Then two small crabs (6-8 cm) somehow got into the cage; one was allowed to remain for the next two months (July to September). In mid-July I observed that this cage contained a dense population of large Mulinia (14,700 individuals/m² with a mean length of 13.4 mm in another empty cage set out in May and sampled in July). Four days later, I observed the two crabs and hundreds of empty and broken Mulinia shells in the cage. The crab that was allowed to remain grew considerably in the next 2 months (to 13 cm carapace width). No Mulinia were found in samples from this cage in September 1974 (Fig. 7J). In contrast, the empty cage sampled at this time was so densely packed with Mulinia (7950/m², 18.2 mm mean length) that some of the clams were sitting on top of each other (Figs. 10, 11). In fact, 4 days after this cage had been removed, exposing approximately 2,000 clams to crab predation, the sediment surface was littered with empty and broken shells, and not one live Mulinia could be found.

In November 1974 and February 1975, empty cages also full of Mulinia were sampled. After the cage was removed and the samples taken, the cage was put back so that approximately half of the Mulinia were within the cage and half were outside the cage. At both of these times, crabs were not feeding in shallow parts of the estuary and nearly all clams survived both inside and outside the cages. In late April 1975, when crabs first started to appear, a few broken Mulinia

shells were found outside these cages and one crab was observed carrying off a large Mulinia. By the middle of May, no live Mulinia could be found outside the cages, while most of the Mulinia inside the cages survived until August and some until September 1975, when the mesh of the cages corroded, holes appeared, and crabs were seen inside the cages. At this time the Mulinia were 16 months old. Most were 22-23 mm; the largest was 26.3 mm, much larger than is ever found in natural habitats. J. Krauter (personal communication) has grown Mulinia in the laboratory to over 30 mm in less than a year. Thus, it appears that Mulinia is a favored food of blue crabs and that crab predation is probably the major factor controlling the adult population size during warmer months.

Mya arenaria (Linnaeus)

The soft clam Mya arenaria spawns in spring and fall. The spring set is usually unsuccessful, presumably because of predation (Wass et al. 1972). In this study, juvenile Mya (0.5-5 mm) were found only in May, November, December, and February. The spring set was much larger than the fall set, but no Mya were found outside the cages from June through October 1974 (Fig. 4R). During this same period, however, Mya survived well in the empty cages and grew rapidly there. Every empty cage in place during one of the spawning periods of Mya had more individuals than outside the cages (Table 7; Figs. 5K, 6N, 7K). The empty cage in place from November 1973 to May 1974, during the larger spring spawning period, had an unusually dense set (over 65,000/m²) of small Mya (1.2 mm mean length) (Table 7). An empty cage set out at the same time (November 1973) and sampled in November 1974 also had a dense set of Mya (over 3000/m²), but these were all

small juveniles (2.0 mm mean length) and were all from the fall 1974 set. It is not known whether this cage had contained any of the Mya from the spring set, or whether there had been a large spring set as in the other cage with the Mya all dying during the summer. Two small crabs (6-7 cm) removed from this cage, one in June and one in September, possibly ate the Mya.

All of the empty cages set out in May 1974 had more Mya than outside the cages (Table 7). The empty→crab treatment sampled in September had no Mya, but there were many broken Mya shells on the surface after the crabs got in. Empty cages set out at the same time as the empty→crab treatment had Mya densities of 388/m² in July (when the crabs got in) and 232/m² in September.

The spot, hand, and crab treatments were all effective in eliminating Mya (Figs. 6N, 7K); the hogchoker was not as effective (Fig. 5K). Samples from any cage containing a crab never contained more than one Mya. Like Mulinia, Mya is a favored food of blue crabs, and crab predation is a major factor controlling Mya abundance.

Lyonsia hyalina Conrad

Only one individual of the lyonsiid bivalve Lyonsia hyalina was found in samples from outside the cages. Empty cages set out in May 1974 had highly significantly ($\alpha < 0.01$) more Lyonsia than outside cages in July and significantly more in September 1974 (Figs. 6 O, 7 L). There were no Lyonsia in samples from the empty→crab treatment in September. Average lengths of Lyonsia in empty cages were 0.5 mm in May, 15 mm in July, 22 mm in September, and 24 mm in November.

Lyonsia live close to the sediment surface, often with the valves sticking partially above the sediment. Thus, like Mulinia,

they are easily preyed upon by crabs. Like Mulinia and Mya, Lyonsia abundance is controlled by blue crab predation.

DISCUSSION

The effect of predation on a community depends on the severity and selectivity of the predation. Low-level predation pressure may increase species diversity by (i) reducing the density of the dominant species, thus allowing for an increase in density of competitively inferior species (Paine 1966, 1969, Brooks and Dodson 1965); (ii) randomly reducing most species densities to a level below that regulated by competitive exclusion of species (Dayton and Hessler 1972, Roughgarden and Feldman 1975); or (iii) creating patches with lowered densities at different stages of succession to a hypothetical "climax community," thus creating "contemporaneous disequilibrium" (Hutchinson 1961, Levin and Paine 1974, May and MacArthur 1972, Horn and MacArthur 1972).

Sufficiently severe predation pressure will decrease species diversity by reducing population densities of all species (Sammarco et al. 1974), rarer species thus being eliminated or reduced to densities too low to be sampled. Effects of predation may be most drastic in physically controlled environments, since the prey organisms must give adaptive priority to the physical regime, rather than to refinement of biological interactions (Slobodkin and Sanders 1969, Sanders 1969).

In the community studied, increasing predation pressure caused a slight decrease in species diversity, and decreasing predation pressure below natural levels allowed a large increase in diversity, indicating that natural predation pressures are severe.

Density-dependent Interactions

The theory of competitive exclusion (Gause 1934) predicts that if two species compete for the same limited resource, one species will eliminate the other. However, predation can alter the outcome of competition between two species in such a way that two species can continue to coexist in a space in which only one could exist without predation (Slobodkin 1961, Brooks and Dodson 1965, Paine 1966, Cramer and May 1972, Levin and Paine 1974, Roughgarden and Feldman 1975). Smith et al. (1975) concluded that the competitive exclusion principle has only limited validity and that, given certain conditions, any number of consumer species may coexist and compete for the same food. Competition for space, food, and light has been demonstrated in marine benthic environments between intertidal barnacles (Connell 1961a, b), between algae (Dayton 1971, 1975a, b), between deposit-feeding mud snails (Fenchel 1975), and between tube-building and burrowing polychaetes (Woodin 1971, 1974).

Herbivores are frequent exceptions to the influence of density-dependent competition, but rather are often predator-limited (Hairston et al. 1960). In an analogous manner, energy for deposit feeders may be available as detrital organic matter in a large "sink" (Levinton 1972, 1974) often three to four orders of magnitude greater than required (Smith 1973). However, much of this organic matter is refractory (Young 1968), and bacteria may be the rate-controlling step in utilization of the organic matter (Fenchel 1975), causing deposit-feeders to be food-limited (Levinton 1972).

In the community studied here, densities of most species increased when protected from predators and no species decreased in density. This lack of preferential increase of any species, including

tube-builders vs. burrowers, suggests that competitive pressures are not important in the regulation of population densities in the natural community. Resources are thus not limiting in these shallow sand communities in Chesapeake Bay. Most species densities in this community are controlled by density-independent factors: predators, sediment instability, and other physical factors.

At the extremely high population densities found in some exclosures, competition probably occurred. For example, at a density of 140,000/m² in one exclosure, individuals of Streblospio benedicti were an average of only 3 mm apart and had almost totally overlapping feeding radii (the tentacular palps extend 10-20 mm along the sediment surface). In some exclosures, Mulinia lateralis were so dense that they could not all fit in a single layer (Figs. 10, 11), and apparently competed with each other for space as they grew (Fig. 9A,B).

In such great density, Mulinia apparently also competed with other species; e.g., Heteromastus filiformis densities were much lower in exclosures with dense Mulinia than in exclosures with fewer Mulinia. This exclusion of other species by Mulinia may have been due to (i) filtering out settling larvae while filter feeding (predation), or (ii) sediment instability caused by Mulinia's active movements (amensalism), or (iii) occupying most available habitat space (competition).

Some Problems of Interpretation

Effect of an empty cage

It is difficult to distinguish the extent to which the increase of infaunal density and diversity in exclosures is caused by (i) exclusion of predators, (ii) changes in currents and sediment stability,

or (iii) "trapping" of larvae. The exclusion of predators has been stressed above, but other factors may also be important.

The cages did affect sediment stability as shown by the increase of silt-clay content and decrease of movement of orange-painted sediment in the exclosures. However, some of this enhanced sediment stability may have been due to increased binding and stabilization of sediments by the dense populations of infaunal tube-building species (e.g. by Streblospio benedicti) forming a "turf" (Buchanan 1963, Young and Rhoads 1971).

Orth (in press) has shown that eelgrass, Zostera marina, increases sediment stability, which causes an increase in infaunal density and diversity. Part of this increase in the infauna may be due to the partial exclusion of predators by the rhizome mat 1-2 cm below the sediment surface which prevents digging by most predators. Infaunal density and diversity increased in eelgrass when predators were excluded; however, this increase was less than when predators were excluded from bare sand. Both eelgrass and exclosures in bare sand produced similar high-density, diverse infaunal communities (Table 8); both stabilize sediments and offer protection from predators.

Planktonic larvae may have preferentially set in cages in response either to decreased current velocity or to contact with the wire mesh. However, while cages may increase setting of larvae, their survival is not ensured--a predator would negate this effect.

Effect of a predator

It is likewise difficult to distinguish the exact nature of the causes of the decrease of infauna due to a predator: (i) predation

TABLE 8

A comparison of infaunal densities in eelgrass, Zostera marina, beds with caged areas in the eelgrass, and caged areas in bare sand.

Numbers from eelgrass are rarefied so that all numbers are reported as mean number per 0.005 m².

	Mean density per 0.005 m ²		
	Caged eelgrass	Uncaged eelgrass	Caged bare sand July-Sept-Nov mean
Total Individuals	264.8	201.6	213.4
Number of Species	20.1	19.0	17.7
<u>Peloscolex gabriellae</u>	41.4	41.1	53.0
<u>Heteromastus filiformis</u>	27.9	21.6	37.3
<u>Streblospio benedicti</u>	26.7	12.5	18.7
<u>Spiochaetopterus oculatus</u>	52.3	28.3	2.4
<u>Nereis succinea</u>	7.8	7.9	4.7
<u>Polydora ligni</u>	130.7	5.1	6.8
<u>Glycinde solitaria</u>	1.9	1.0	3.7

on adults (implicitly stressed above), (ii) predation on newly-set larvae, (iii) decreased sediment stability caused by the foraging activities of the predators, or (iv) physical disruption of tubes and burrows.

The incompletely answered question is whether the cage causes sediment stability which in turn allows an increase of infauna, or whether the cage excludes predators which allows an increase of infauna which stabilizes sediment. To better differentiate the biological and physical aspects, more careful analyses of predators' feeding activities and sedimentary parameters are necessary. Aquaria could be used for observation of feeding modes and preferences, and for verification of results of caging experiments.

Effect of cage size

The size of cages was varied in order to vary crab densities, rather than directly varying the number of crabs in the standard size cage; otherwise cannibalism would have been a problem. Thus both the size of the cage and the area over which a crab could roam was different for each crab density. Therefore part of the effect of the different crab densities may have been due to cage size. However, empty cages of two different sizes were not different from each other for number of species, number of individuals, or individuals of most species (Fig. 5). Therefore, differences in the infauna in different-sized cages with crabs were probably due to the different crab densities rather than to different sizes of cages.

Effect of cage mesh size

Although cages did keep out most large predators, many smaller individuals of many predatory species undoubtedly had free

passage through the 12 mm mesh of the cages. Naqvi (1968) concluded that 6 mm mesh cages offered more protection from predators in Alligator Harbor, Florida, than 12 mm or 24 mm mesh cages. However, the larger individuals of the species I studied (blue crab, spot and hogchoker) were effectively caged in or out, and these larger individuals of blue crabs and spot are apparently the major predators in the area studied.

Susceptibility to Predation

While there was a large variation among species in the degree of response to altered predation pressure, species with similar life habits responded similarly.

Least affected by increased crab and fish predation pressure were those species which live deep in the sediments and/or can retract quickly into the sediments. Species surviving in greatest numbers in cages containing crabs were Peloscolex gabriellae, Spiochaetopterus oculatus, Phoronis psammophila, large Mya arenaria, Heteromastus filiformis, and Streblospio benedicti. Included here are the five top-ranked species in the natural community (Table 1), suggesting that avoidance of predation allows their success. Such protective habits have also evolved in other shallow-water invertebrates in response to predation by fishes (Bakus 1964, Levinton 1971).

Species whose densities were most severely reduced by predators were larger animals living close to the sediment surface, e.g. the polychaete Pectinaria gouldii and the bivalves Mulinia lateralis, Lyonsia hyalina, and small Mya arenaria. Blue crabs could also dig up deep-living Mya (Dunnington 1956, Orth, in press). For example, in the empty+crab treatment the invading blue crabs presumably

eliminated all the Mulinia and the Mya, which were fairly large (25 mm mean shell length) and probably lived 50-60 mm deep in the sediment.

Some species of bivalves are abundant presumably because they can avoid crab predation by either of two methods: (i) living too deep for crabs to dig (e.g. large Mya arenaria, and perhaps Macoma spp.), or (ii) having a shell too thick (as adults) for crabs to break (e.g. Mercenaria mercenaria, Rangia cuneata, and Crassostrea virginica).

However, none of these mechanisms offers safe refuge from cow-nosed rays, Rhinoptera bonasus, which are significant predators of large deep-burrowing and heavy-shelled bivalves over extensive areas of Chesapeake Bay (Orth 1975). Crab and ray predation may be responsible for the relative lack of bivalve dominance in infaunal communities in Chesapeake Bay. Muus (1973) concluded that predation was the dominant cause of juvenile bivalve mortality in the Øresund, Denmark.

Large individuals of many species are cropped by predators and never grow to their maximum attainable size. Mulinia lateralis, Lionisia hyalina, and Pectinaria gouldii grew to a much larger size in enclosures in only a few months than is found in natural sediments outside cages. The very rapid growth rates and absence of large individuals implies that for many species there is more than one generation per year.

Trophic group amensalism (Rhoads and Young 1970) may be responsible for some filter-feeding bivalve mortalities in summer. Turbidity becomes higher in summer (Patten et al. 1966), presumably due to greater resuspension of bottom materials (Oviatt and Nixon 1975) reworked by deposit feeders (Young 1971, Rhoads and Young 1971, Aller and Dodge 1974). This biologically-induced higher

turbidity adversely affects filter-feeding organisms by clogging filtering and respiratory surfaces, and may cause the demise of dense populations in muddy sediments (Levinton and Bambach 1970, Rhoads 1974, Boesch, Wass, Virnstein, in press, Peddicord, in press a, b). In sandy areas, however, since Mulinia survived in exclosures through two consecutive summers, it was obvious that blue crab predation limited survival in the natural community.

Species exhibiting the largest population increases in response to decreased predation pressure were the opportunistic species Streblospio benedicti, Heteromastus filiformis, Polydora ligni, and Mulinia lateralis. Young and Young (1975) also found that the species which showed the largest increases in density inside mesh exclosures in a coastal lagoon, the Indian River, Florida, were the opportunistic polychaetes Capitella capitata and Polydora ligni.

Diversity, Stability, and Opportunistic Species

It has generally been accepted that diverse communities with complex food webs and alternate trophic pathways are inherently more stable (MacArthur 1955, Emlen 1973, Malay 1975, Smith 1975). Rather, it is environmental constancy that allows a diverse community to develop (Sanders 1968). While diverse communities may be more constant over time ("persistent"), they are not necessarily more stable in terms of resisting change due to perturbations ("resistant") or of recovering from such changes ("resiliency") (Boesch 1974).

Recent evidence suggests, however, that trophic complexity and diversity of community interactions does not lead to greater stability (May 1973, Boesch 1974, Malay 1975, Peterson 1975, Steele 1974). Older more diverse fields were experimentally found to be less

stable when perturbed by fertilization (Hurd and Wolf 1974). Estuarine ecosystems are characterized by environmental stress and inconstancy, and although they may lack persistence, they have high resistance and resilience (Boesch 1974), as shown by the resistance and quick recovery of the benthos of Chesapeake Bay when subjected to severe flooding (Boesch, Diaz, Virnstein, in press). Estuarine systems are already subjected to energy-requiring stresses and are more likely to resist changes than those adapted to relatively constant environments (e.g. tropical ecosystems) (Copeland 1970).

Opportunistic eurytopic species play a large role in response to disturbances, and are abundant in most Chesapeake Bay habitats (Boesch 1973, in press), indicating stressed or disturbed environments, characteristic of most estuaries. These r-strategists are able to react rapidly to changing environments, temporarily open space, and relaxed predation pressures (Boesch, in press, Boesch, Diaz, Virnstein, in press, Grassle and Grassle 1974, Levinton 1970). Pollution may also exclude predators in a manner similar to experimental exclosures, allowing densities of these eurytolerant opportunistic species to increase (Young and Young 1975).

Opportunistic species played a large role in the community studied. Two of the top-ranked species, Heteromastus filiformis and Streblospio benedicti, acknowledged opportunists (Grassle and Grassle 1974), were among the most abundant species in natural sediments and in cages with crabs. Together with the opportunistic Mulinia lateralis, these species were dominant in most exclosures, with densities one to two orders of magnitude greater than outside exclosures.

IMPLICATIONS

Species populations in the community studied are not resource-limited as has been found in other marine communities, both on hard substrates (Dayton 1971, Connell 1972) and in soft sediments (Woodin 1974). Predation pressures and physical disturbances are severe in this community and keep population levels far below the carrying capacity of the environment. At these lowered densities, competitive interactions, both inter- and intra-specific, are relatively unimportant. Physical factors, such as sediment instability (Orth, in press, Aller and Dodge 1974), changes in salinity and temperature (Boesch, Wass, Virnstein, in press), and high turbidity, together with severe predation pressures stress the community. The community structure is not controlled by processes operating exclusively within the benthos; rather, this infaunal community is controlled by factors external to the infauna. In this community, the patterns of species occurrence and density are disproportionately affected by the activities of a single species of high trophic status-- Paine's (1969) definition of a "keystone species". The blue crab Callinectes sapidus fits this definition.

A corollary of the conclusion that predators are important to the benthic community studied is that this community is important to the predators. Secondary productivity is probably very high with two or three generations per year for many species and a biomass of

7 g/m² (wet weight) (Virnstein 1975). The annual turnover rate of the macrobenthos of Kiel Bight in the Baltic Sea is one to several times the mean biomass, most of which is consumed by commercial fish (Arntz and Brunswig 1975). A similar relationship probably exists in Chesapeake Bay, except that growth and production rates in Chesapeake Bay are greater than in the Baltic and other northern areas. Growth rates for bivalves in the Baltic (Muus 1973) are much slower than found in this study. For example, two year old Mya arenaria are only 28 mm long in the southern Baltic (Munch-Petersen 1973), 20 mm in the Bay of Fundy (Newcombe 1935), and 80 mm in Chesapeake Bay (J. Lucy, unpubl. data). Mature Mulinia lateralis (10-15 mm) are 1-2 years old in Long Island Sound (Calabrese 1969); this size is attained in only 2 months in Chesapeake Bay (Fig. 9A). Cephalic plate width (a standard measure of overall size) of Pectinaria hyperborea in St. Margaret's Bay, Nova Scotia 1 year after setting was 4 mm (Peer 1970), 3 mm for P. californiensis in Puget Sound (Nichols 1975), and 7 mm for P. gouldii after only 4 months in Chesapeake Bay (this study). Although growth rates of these three species are not necessarily comparable, all attain a similar maximum size. Both Nichols and Peer reported an annual production to mean biomass ratio of 4.3 for Pectinaria. Turnover ratios would be greater in Chesapeake Bay due to faster growth and low population densities, thus providing a potentially larger food supply for bottom-feeding fishes and crabs.

Hayne and Ball (1956) found that although the standing crop of bottom fauna in ponds was decreased in the presence of bottom-feeding fishes, the rate of production of the bottom fauna increased.

They reported the average production of bottom fauna during a growing season to be approximately 17 times the standing crop, when fish were present. Thus, the heavily preyed-upon infauna of shallow, sandy areas studied here may be more important in terms of crab and fish food production than the higher density, but less preyed-upon, infauna of grass beds. In grass beds, predators apparently prey more heavily on epifauna than infauna (Orth, in press, Young and Young, in press).

Since food and space are not limiting, resources are underutilized and a much greater biomass could be maintained (properties characteristic of low-diversity ecosystems) (Odum 1971). If protected from predators, much larger standing crops of infaunal bivalves could be raised as food for man, as is done for epifaunal oysters.

In summary, such shallow water infaunal communities are highly stressed; species populations are not resource-limited, but rather are predator-controlled, and these communities are an important food source for predatory species important to man.

The degree of importance attributed to predators as determined by this study could probably not have been determined by other than experimental methods. Any merely correlative non-manipulative studies could not have determined the effects of increasing or decreasing predation pressure--proper controls are simply not available. Just as the experiments of Connell, Dayton, Paine, and others in the rocky intertidal zone have demonstrated the importance of both physical and biological interactions, more experimental works such as Woodin (1974), Orth (in press), and this study in soft-sediment communities, though inherently more difficult, are necessary.

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